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North by northwest: climate change and directions of density shifts in birds

Running head: Climate change and direction of density shift

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Abstract

There is increasing evidence that climate change shifts species distributions towards poles and mountain tops. However, most studies are based on presence-absence data, and either abundance or the observation effort have rarely been measured. In addition, hardly any studies have investigated the direction of shifts and factors affecting them. Here we show using count data on a 1000 km south-north gradient in Finland, that between 1970–1989 and 2000–2012, 128 bird species shifted their densities, on average, 37 kilometres towards the north northeast. The species-specific directions of the shifts in density were significantly explained by migration behaviour and habitat type. Although the temperatures have also moved on average towards the north northeast (186 kilometres), the species-specific directions of the shifts in density and

temperature did not correlate due to high variation in density shifts. Findings highlight that climate change is unlikely the only driver of the direction of species density shifts, but species-specific characteristics and human land use practices are also influencing the direction. Furthermore, the alarming results show that former climatic conditions in the northwest corner of Finland have already moved out of the country. This highlights the need for an international approach in research and conservation actions to mitigate the impacts of climate change.

Keywords: distribution changes, ecological traits, global warming, habitat selection, monitoring censuses, species distribution models.

Introduction

Understanding the impact of climate change on species populations is a fundamental question to mitigate the effects of changing climate. There is an increasing body of literature showing that species of various taxonomic groups including plants, invertebrates and vertebrates in both northern and southern hemisphere of the globe have shifted their distribution during both summer and winter season likely due to climate change (Parmesan *et al.,* 1999; Parmesan & Yohe, 2003; Hickling, *et al.,* 2006; Kelly & Goulden, 2008; Zuckerberg *et al.*, 2009; Booth *et al.,* 2011; Chen *et al.,* 2011; La Sorte & Jetz, 2012; Breed *et al.,* 2013; Pearce-Higgins & Green, 2014). Although there is some evidence that species-specific characteristics, such as habitat preferences, affect how species are responding to climate change (Pöyry *et al.*, 2009) it is still largely poorly known what factors drive the variation in species-specific responses.

Distribution changes are typically examined at the edges of the distribution using presence-absence data often ignoring the importance of survey effort (Kujala *et al.,* 2013), whereas changes in the central gravity of the populations using abundance data has much less frequently been examined (Maclean *et al.*, 2008; Lehikoinen *et al.,* 2013; Virkkala & Lehikoinen, 2014). Furthermore, majority of the studies have only investigated shifts directly towards the poles despite the fact that isotherms are rarely placed linearly along latitudes in nature (Huntley *et al.,* 2007, see also Fig. 1). Therefore, predicted distribution changes of species have also been suggested to occur nonlinearly towards the poles (Huntley *et al.,* 2007; Burrows *et al.,* 2013). Interestingly, the direction of the distribution changes has often been neglected (Gillings *et al.,* 2015). This could underestimate the distance in species distribution

63 changes (Gillings *et al.,* 2015) as most of the earlier studies have often looked at only
64 on one dimension of the shift (e.g. Thomas & Lennon, 1999; Thomas, 2010).
65 Hockey *et al.* (2011) studied the direction of the species distribution changes in
66 South Africa using only cardinal directions. On the other hand, Gillings *et al.* (2015)
67 investigated the actual direction of the shift using presence-absence data from UK. In
68 view of conservation, it is more important to investigate the changes in species
69 abundance than occurrence only, as presence-absence data can mask changes in
70 species abundance (Virkkala & Lehikoinen, 2014). To our knowledge, the directions
71 of the species' density shifts using long-term abundance data over decades have not
72 been investigated before. However, Tayleur *et al.* (2015) investigated directions of
73 density shifts of Swedish birds in 21st century and found that shifts were poorly
74 connected with climatic variables. Furthermore, the impact of potential other
75 ecological factors than climate on the species-specific variation in the direction of the
76 density shifts have not been examined.
77 Here we investigate, based on 128 Finnish birds species, the general direction in
78 shifts of species' central gravity of abundance (hereafter density shift), and whether it
79 is linked with the direction of the temperature change. Our hypothesis is that
80 directions of the species-specific temperature and density changes would correlate to
81 support the impact of climate change as the key driver of distribution changes.
82 Furthermore, we investigate whether the direction of the shift differs between
83 functional ecological species groups. We compare density shifts in 147 50-km grid
84 cells between two periods: 1970–1989 and 2000–2012.
85 We used three different categorizations of species: (i) distribution type, (ii)
86 habitat type and (iii) migration strategy. We used these groups, because (i) northern
87 species have shifted their densities toward the north at a faster rate than southern

88 species (Virkkala & Lehikoinen, 2014). We therefore predict that northern species
89 would show density shifts towards more northerly directions than southern ones, and
90 the more diverse distribution of directions among southern species would thus explain
91 the slower speed of density shifts. (ii) Potential habitats for farmland, urban and
92 montane species are highly restricted, and the first two ones are highly influenced by
93 human activities, as e.g. farmland practices have strongly affected farmland bird
94 population trends in Europe including Finland in recent decades (Donald *et al.*, 2001;
95 Laaksonen & Lehikoinen, 2013). Our hypothesis is that forest species would show
96 density shifts to more northerly directions than farmland and urban species. Arable
97 land in Central Finland is concentrated especially on western part of the country
98 (Ostrobothnia area), which could cause a more western direction of density shifts in
99 farmland species compared to other species groups. (iii) In residents and partial
100 migrants a substantial proportion of the individuals remain in the breeding areas and
101 can thus better track directly changes in their breeding environment compared to
102 migratory birds, which are also affected by changes on their migratory route and
103 wintering grounds. European long-distance migrants especially have declined
104 substantially in recent decades (Sanderson *et al.,* 2006; Laaksonen & Lehikoinen,
105 2013). In addition to migration distance, the migration direction may affect the
106 direction of the density shift. Finnish birds have several migration directions from
107 West Africa to East Asia, and since species are migrating from different directions,
108 this can affect their direction of the density shift. We predict that southwest, south and
109 southeast migrants would show density shifts towards northeast, north and northwest,
110 respectively.
111
112

Materials and methods

Census data and calculation of relative densities

Line transects have been conducted in Finland regularly since the 1970's (Virkkala & Lehikoinen, 2014). The line transects are one-visit censuses in which birds are counted along a transect with a length typically 3–6 km, and the locations of the transects have been placed on a map in advance (Lehikoinen *et al*, 2014; Virkkala & Lehikoinen, 2014). The methodology is suitable for counting birds over large areas, and the line transect census can be used to investigate relative densities of species (Järvinen & Väisänen, 1975, 1981). The census period is June and the counts are carried out earlier in southern Finland (between June 1–20) compared to northern Finland (between June 10–30) due to later breeding phenology in northern latitudes. Transects were censused during early morning, when the singing activity of birds is highest in dry weather conditions. The observer walks alone at a speed of 45–60 min/km depending on the density of birds along the route using a map, compass or GPS. Each observation is classified as one of the five following categories: (i) singing or displaying, (ii) other calls, (iii) sightings (male, female, pair, brood or nest), (iv) flying bird and (v) flying flock. Flocks are transformed into pairs, normally by dividing by two (male and female) plus the mean species-specific brood size in case of brood flocks. The census unit is a pair of birds, not an individual; thus a male and a female seen separately or together, or a parent with offspring, is transformed into one pair (see Järvinen *et al.,* 1991). The line transect is divided into a main belt and a supplementary belt. The main belt is 50 m wide (25 m on both sides of the transect line) and the supplementary belt is beyond the main belt as far as birds can be

138 detected. Every observation is placed either on the main belt or on the supplementary
139 belt. Birds crossing the main belt belong to the supplementary belt even if first
140 observed above the main belt. Together, the main belt and the supplementary belt
141 form the survey belt. An earlier study showed that species-specific annual proportions
142 of displaying birds and birds in the main belt were stable during 1987–2010, which
143 indicates that there are no major changes in species detectability (Lehikoinen, 2013).
144 We divided Finland into 50-km grids and calculated how many kilometres of
145 line transects have been conducted in each grid during the two different periods,
146 1970–1989 and 2000–2012 (on average 25 years apart). We omitted the 1990s, since
147 this period has slightly poorer coverage than other decades in some parts of the
148 country. Nevertheless, the decadal data has shown that abundances of the 94 most
149 common species shifted progressively toward higher latitudes (Virkkala &
150 Lehikoinen, 2014). Altogether 147 grid cells, covering most parts of the country,
151 included at least 10 kilometres of line transects during both the periods (see Fig. 1a).
152 During our study periods of 1970–1989 and 2000–2012, altogether 303,647 and
153 490,474 pairs of birds were observed, respectively. 128 species having at least 20
154 observations during both periods were included in the analyses (Supplementary
155 Table 1).
156 We calculated species-specific densities for each grid, based on the number of
157 pair observations and the length of the line transects in each block and species-
158 specific correction coefficients (Järvinen & Väisänen, 1983). The relative density of a
159 species (D, pairs/km^2, hereafter density) based on the Finnish line transect census was
160 calculated as:
161 $D = K \times N/L,$ (1)

where K = species-specific correction coefficient, N = numbers of pair observations of a species on the whole survey belt, and L = transect length (in km). Species-specific correction coefficients are based on distance sampling, where ratios of bird observations on the main belt to those on the supplementary belt are used to calculate densities of species in a larger (survey belt) line transect (Järvinen & Väisänen, 1983). We used the earlier published correction coefficients (Virkkala & Lehikoinen, 2014, Supplementary Table 1) and, using the same data, calculated correction coefficients for the additional 34 species that were not included in the earlier study (Supplementary Table 1).

Järvinen & Väisänen (1983) have presented correction coefficients based on data prior to the 1980s. However, since then a lot of new data have been gathered, so we have revised the coefficients. We calculated species-specific correction coefficients for southern and northern Finland (divided by the 710 latitude in the Finnish coordinate system) and for the whole country based on the whole of the Finnish monitoring data since the 1970s, when both the main belt and the supplementary belt had been used. The species-specific correction coefficient (K) was calculated as (Järvinen & Väisänen, 1983):

$$K = 40 - 40 \sqrt{(1-p)}, \quad (2)$$

where p = proportion of main belt observations (range 0–1); for details of the calculations, see Järvinen (1976) and Järvinen & Väisänen (1975, 1976a, 1983). Observability of species is also affected by the overall density of bird specimens. The higher the total bird density, the lower the observability on the supplementary belt (see Järvinen & Väisänen, 1976b). This can be corrected by studying the number of observations on the main belt. Therefore we also used density dependent correction coefficient (y) calculated as (see Järvinen & Väisänen, 1983):

$$y = 0.0320x + 0.684 \quad (3)$$

where x is the number of main belt observations of all species per km. The correction coefficient (y) receives values above one in regions of high main belt density and below one in regions of low density. Thus, the density values calculated (equation 1) were multiplied by the density dependent correction coefficient (y) (Järvinen & Väisänen, 1983). The density dependent correction coefficient was calculated separately for each 50-km square for both periods.

We used these grid-specific densities to calculate arithmetic central gravity of densities for each species during both the periods. This was done by first calculating the northern latitude using mean densities per each latitude grid row (Virkkala & Lehikoinen, 2014) and then calculating the longitude using mean densities per each grid column (species-specific density maps and central gravity of densities are shown in Supplementary Figs 1–128). In addition, gravity of densities was affected by the location of censuses inside each grid. The point of each grid cell used in the analyses was calculated based on mean coordinates of all line transects conducted in the grid during that particular period. We preferred arithmetic mean instead of median or geometric mean, since using median the shift would be occurring mainly on grid level in compass points and intercardinal directions, whereas arithmetic mean allows higher resolution in direction of the shifts. We declined to use geometric mean, since many grid cells have zero values which complicates the calculation of geometric mean.

Based on latitude and longitude it was possible to calculate direction and distance of the density shift of species between the two periods. Direction in degrees could be calculated using inverse hyperbolic tangent and distance using Pythagoras' Theorem.

We divided species into groups using four different classifications (Supplementary Table 1). First, we divided species into groups based on their general distribution (southern edge and northern edge species and species which occur in the larger part of country). This was done using the bird atlas data from Finland from 2006–2010 (see Valkama *et al.,* 2011). Southern and northern species, which had been observed in less than 20% of the grid cells in Finland during this atlas period, were classified as edge species. Rest were classified into one group that inhabit larger geographic areas. Second, we divided species into four categories based on their habitat use: farmland-urban, forest, wetlands (including rocky outcrops) and montane (Virkkala *et al.,* 1994; Väisänen *et al.,* 1998; Laaksonen & Lehikoinen, 2013). Third, species were classified into four groups based on their migration distance (residents, partial migrants, short- and long-distance migrants (Cramp *et al.,* 1977–1994; Valkama *et al.,* 2014). We first divided species into two groups, residents-partial migrants and true migrants (short- and long-distance migrants) and later performed a more detailed analysis where all four groups were included. Last, we divided species into three groups based on their main migration direction: southwest (wintering in West Europe and West Africa), south (South and Central Europe, South and East Africa) and southeast (Southeast Europe and Asia (Cramp *et al.,* 1977–1994, Valkama *et al.,* 2014). There was no strong collinearity between groups (all $|r| < 0.27$).

The general direction of density shifts could also be caused by the geographical shape of Finland, since the shape of the country is not a rectangle. We investigated how this could affect the direction of the density shifts by moving densities of the grid cells directly towards north. We moved the densities of the first period one grid northwards (except the most southernmost grids which remained similar) to mimic the northwards density shifts. In cases where the grid did not have density value on the

236 southern side, we used mean density values of the nearest southwest and southeast
237 side of the grid (Supplementary Fig. 129). We did these movements of densities for
238 each species and calculated the direction of density shifts similarly as in the observed
239 density shifts of species, and thus calculated the hypothetical density shift of each
240 species.
241 The temperature data originates from the Finnish Meteorological Institute and
242 included daily values in 10-km grid cells (Fig. 1b). We calculated mean temperatures
243 for 50-km grids used in the analyses of bird data during the two study periods.
244 Furthermore, we searched, using temperature of the first period for each 50-km grid,
245 where the nearest as cold grid cell within Finland was located during the second
246 period. Based on this information we could calculate which direction the climate has
247 shifted regionally (Fig. 1c), and thus what would be the direction that species should
248 have shifted to remain in the same climatic conditions. Last, for each species we
249 calculated the mean direction and distance of the temperature change from the grid
250 cells where the species had been observed in the first study period.
251
252 Statistical analyses
253
254 All the statistical analyses were conducted in Matlab R2014a. Significance of the
255 species-specific density shifts along compass directions and impact of sampling effort
256 and temperature were tested using log-linear Poisson regression model
257 $N = L + Temp + Latitude + Longitude$ (4),
258 where the grid specific change in the number of observed pairs in grid cell (N) is
259 explained by corresponding change in the length of the line transect (L), temperature
260 (Temp), latitude and longitude of the same grid cell.

The species-specific directions of the density shifts were calculated by using inverse tangent (Matlab function atand) and by using the values of the Finnish uniform coordinate system, where a change of one unit corresponds distance of 10 kilometres (see Fig. 1). For circular analyses, Circular Statistics Toolbox was used. All the functions of the toolbox and their codes are freely available on the web (Berens, 2009). The mean direction was calculated using the function circ_mean and the 95 % confidence intervals were calculated using the function circ_confmean. Rayleigh's test (function circ_rtest; test for the significance of the mean direction in the cycle histogram) was used to test whether the directions differ from an even distribution. Furthermore, the Harrison-Kanji test (function circ_hktest; circular analog of two-factor ANOVA) was used to analyse whether the direction of different groups differed. The Watson-Williams test (function circ_wwtest; circular analog of the one-factor ANOVA) was used to test whether the direction of temperature and density shifts differed, and the function circ_corrcc was used to test whether the species-specific directions in temperature and density correlate. Last, because closely related species may show similar type of responses, we investigated whether the findings were linked to the phylogeny of the species. We tested whether the residuals of results were correlated with the relative phylogenetic distance on the order and family level. We did this by correlating the differences in residuals of a pair of species with the corresponding relative phylogenetic distance between the species. The phylogeny was based on the taxonomy of AERC TAC (http://www.aerc.eu/tac.html). Function circ_corrcl was used to test the potential influence of phylogeny by correlating the differences in residuals of each pair of species with the corresponding relative phylogenetic distance between the species. In addition, the average direction

and distance of shifts (vector) was calculated by using the arithmetic mean of a species' latitude and longitude change.

Since the analyses of the significance of the density shifts (128 tests per variable) and the investigation of impacts of different groups required multiple testing (5 tests) we used a sequential Bonferroni correction to adjust the P-values (Rice, 1989).

Results

The findings show that the mean direction of the density shift was on average towards the north northeast ($\alpha = 12°$, 0° is north with rotation clockwise). The distribution of directions differed significantly from an even distribution (Rayleigh's test, $z = 17.7$, $n = 128$, $P < 0.001$), but not from the direct north direction (Fig. 2a). On average, species densities shifted 35.9 kilometres towards the north and 7.0 kilometres toward the east in 25 years (36.6 km in total, 1.5 km / year). However, there was a large variation in the density shift between species. Among the 128 study species, 96 species shifted their densities northward (mean $\alpha = 17°$, north northeast, c.i. 7–27°) with an average of 60.2 kilometres shift north and 18.9 km shift east (mean average total length of density shift of 82.1 km, 3.3 km / year). About half of these species, 49 species, shifted their densities northward more than 50 kilometres, and for only 25 species the shift towards north was less than 20 kilometres (Supplementary Table 1).

Correspondingly, 32 species shifted their densities in the southern directions (mean $\alpha = 216°$, c.i. 197–235°) with an average of 33.8 km shift south and of 34.7 km shift west (mean average total length of density shift of 72.7 km, 2.9 km/ year). Half of these species (16) shifted their densities less than 20 kilometres towards south and only seven species shifted their densities more than 50 kilometres southwards (Supplementary Table 1). The glm test revealed that 63 of the species shifted their densities significantly towards north and 17 significantly towards south (Supplementary Table 1). Correspondingly 11 species shifted their densities significantly towards east and ten towards west. Grid-specific changes in temperature explained only shifts of four species, and changes in length of line transects did not showed significant results.

318 The modelled northwards movement of densities of species produced on
319 average density shift towards the north (α = 9°, c.i. 358–20°), which did not differ
320 either from the direct north or the corresponding observed density shift of species (α
321 = 12°).
322 The mean direction of the temperature shift was north northeast (α = 13°, Fig.
323 2a) and did not differ from mean direction of the species' density shift (Watson-
324 Williams test, $F_{1,254} = 0.02$, P = 0.90). There was however a clear geographical pattern
325 in the direction of the temperate shift. In the southern half of Finland, the direction
326 was on average toward the northeast, whereas in the northern part of the country the
327 temperatures shifted westward toward the mountainous region in the northwest (Fig.
328 1c). In the northwest corner, the climatic conditions of the 1970's and 1980's, in the
329 resolution of 50-km grids, have already moved outside the borders of Finland (Fig.
330 1c). Despite the similar mean direction of both the temperature and density shifts of
331 species, the species-specific directions did not correlate significantly (rho = -0.03, n =
332 128, P = 0.71). Furthermore, the distance of the temperature change was on average
333 186 km (min-max 143–301 km), which is more than five times the mean distance that
334 all species have shifted toward the north.
335 Habitat type and migration distance significantly explained the difference in
336 distribution of directions (Harrison-Kanji test, $\chi^2_2 = 17.92$, P = 0.0064, $\chi^2_6 = 8.84$,
337 P = 0.012, respectively, Fig. 2b-c). Despite the high variation in the directions,
338 farmland-urban, wetland and montane species shifted their densities towards the north
339 northwest (α = 335°, α = 339°, and α = 350, respectively; Fig. 2b-c), whereas forest
340 species moved towards the north northeast (α = 32°, Fig. 2b, Supplementary Fig.
341 130). For instance typical farmland species like Lapwing *Vanellus vanellus,* Skylark
342 *Alauda arvensis,* Barn Swallow *Hirundo rustica* and Eurasian Starling *Sturnus*

343 *vulgaris* shifted their densities more than 40 km westward. In contrast, Eurasian
344 Sparrowhawk *Accipiter nisus*, Osprey *Pandion haliaetus*, Merlin *Falco columbarius*,
345 Red-breasted Flycatcher *Ficedula parva*, Willow Tit *Poecile montanus*, Coal Tit
346 *Periparus ater* and Common Crossbill *Loxia curvirostra* showed the strongest shifts
347 among forest birds towards north and east (all shifted more than 150 km,
348 Supplementary Table 1). Among montane birds, the strongest shifts were observed in
349 Long-tailed Skua *Stercorarius longicaudus* and Lapland Longspur *Calcarius*
350 *lapponicus* which shifted towards northeast more than 100 kilometres and Snow
351 Bunting *Plectrophenax nivalis* whose densities shifted towards the highest mountains
352 in the northwest more than 80 kilometres.
353 Furthermore, when grouping species into residents-partial migrants and true
354 migrants, there was a significant difference in the directions between groups (Fig. 2d).
355 Almost all resident and partial migratory species shifted their densities towards the
356 northeast ($\alpha = 39°$, Fig. 2d), whereas many migratory species showed density shifts
357 towards the west and southwest ($\alpha = 358°$, Fig. 2d, Supplementary Fig. 131).
358 However, a more complicated model with the four migration type categories did not
359 explain species-specific variation in the shift of the densities (H-K test, $\chi^2_6 = 9.54$,
360 $P = 0.15$). This was likely because both residents and partial migrants moved towards
361 the northeast and short- and long-distance migrants towards the north (Supplementary
362 Fig. 132a–d). In the case of either habitat type or the migration distance the residuals
363 of the models were not correlated with the phylogeny either at the order or family
364 level (all P's > 0.26).
365 There was some evidence that migration direction explains part of the variation
366 in density shifts (H-K test, $\chi^2_4 = 11.1$, $P = 0.086$). Species wintering in the southwest
367 shifted their densities on average towards the north northeast direction ($\alpha = 13°$),

368 whereas species wintering in the south and southeast shifted their densities towards
369 north northwest (α = 339° and α = 335°, respectively, Fig. 2e), as would have been
370 expected based on their migration routes. The distribution of the directions did not
371 differ between southern edge (α = 323°) or northern edge (α = 72°) species or species
372 that occur in the large part of the country (α = 8°, H-K test, $\chi^2_4 = 7.12$, P = 0.13;
373 Fig. 2f). In general, the group of species that shifted their densities westwards
374 included several types of species, such as migrants wintering in Asia (e.g. Blyth's
375 Reed Warbler *Acrocephalus dumetorum* and Greenish Warbler *Phylloscopus*
376 *trochiloides*), farmland species (mentioned above), and other species with declining
377 population dynamics (e.g. Common Buzzard *Buteo buteo*, Honey Buzzard *Pernis*
378 *apivorus,* Hen Harrier *Circus cyaneus* and Sedge Warbler *Acrocephalus*
379 *schoenobaenus*) (see Supplementary Table 1).
380
381
382

Discussion

The findings reveal that directions of species' density and temperature shifts are not directly towards the north, but most often towards the north northeast and north northwest. Although these directions can partly be driven by the geographical shape of the country, this underlines that the rate of species density shifts are underestimated, if the shift is only measured using one north-south dimension. However, the speed of the temperature change has been much faster than corresponding speed in the change of bird species densities, which has also been found in some earlier studies both in Europe and North America (Devictor *et al.,* 2008, 2012; La Sorte & Jetz, 2012). Importantly, although the species and temperature had on average the same direction, the species-specific values were not significantly correlated as we predicted. This is probably due to the large variation in the species density shifts, since 25% of the species show a move towards southern directions. In a recent work, Tayleur *et al.* (2015) showed that only 20% of the Swedish bird species had shifted their densities towards the expected direction during 21th century according to the temperature change and changes in rainfall had hardly any impact on density changes. On the other hand, Virkkala *et al.* (2014) showed that observed changes in Finnish bird distributions between 1974–89 and 2006–2010 were largely in the same direction as predicted range shifts by 2051–2080 based on bioclimatic envelope models. Understanding causes of the variation in species-specific directions and the speed of change is crucial for making predictions in species distributions and for conservation actions.

This study shows that forest bird species have on average shifted towards a northeastern direction, whereas species of other habitats have on average shifted their

densities towards northwestern directions. Finland is situated on the western edge of the Eurasian boreal forest zone (see e.g. Huntley *et al.,* 2007; Virkkala *et al.,* 2008), which is why it is logical that forest species show density shift towards the northeast. Nevertheless, management of forest can also affect species ability to move their distributions (Felton *et al.,* 2014). On the other hand, declining montane species (Lehikoinen *et al.,* 2014) were moving on average towards the north northwest, where the highest and coldest montane areas are situated in Finland. Thus, the physiography of Finland explains some of the shifts. Northwards density shifts of bird species have also been observed in Finnish protected areas, where human-caused land use is prohibited, suggesting that climate change was the main cause for species density shifts in natural habitats (forests, wetlands and montane habitats) (Virkkala & Rajasärkkä, 2011). In addition, land use changes also influence our results. Farmland birds have generally declined in Finland since the 1970's, mainly due to changes in farmland practices (Rintala & Tiainen, 2007; Laaksonen & Lehikoinen, 2013). Mean density shifts of farmland species towards a northwestern direction is supported by our predictions, as the largest arable land areas in the northern and central part of the country are situated on the western side. Moreover, densities of several farmland species have shifted towards the southwest indicating that these species have retracted towards their core breeding areas. In the UK, land use changes have been shown to be more important drivers of the farmland bird species than climatic factors (Eglington & Pearce-Higgins, 2012).

Furthermore, migration behaviour, especially the comparison between residents (including partial migrants) and true migrants explained the differences in species-specific variation in the shift direction. Residents and partial migrants shifted their densities very strongly toward the northeast, whereas among migrants, many species

showed western or southwestern density shifts. This could indicate that residents and partial migrants could better track climatic changes than migratory species, which are away for the winter (Pearce-Higgins & Green, 2014).

Many south-eastern and southern migrants tend to spread in western directions, whereas southwestern migrants tend to spread towards the north northeast. Although these groups did not differ between each other significantly, this kind of pattern would make sense as species migration direction classifies the angle along which birds tend to move most during their life cycle. One of the widely known impact of climate change is advanced spring arrival dates of many bird species (Jonzén *et al.,* 2006; Lehikoinen & Sparks, 2010, Vaitkuviene et al. 2015). The advanced spring migration potentially together with more favourable migration conditions could be one of the mechanisms behind climate induced distribution shifts due prolonged to migration distances (Otterlind, 1954; Berthold, 2001). This emphasizes that the migration direction and route of dispersal should be investigated in more detail. However, since our study showed that residents and partial migrants shifted more towards northeast than true migrants other mechanisms are also acting here.

Although this study is based on large-scale data covering over 1000 km in a north-south direction through the boreal zone and over 600 kilometres in a west-east direction, it is still conducted within one country and does not cover the whole population of any of the study species. Such analyses dealing with abundance shifts at a whole population level are very rare (see, however, Lehikoinen *et al.,* 2013: Pavón-Jordan *et al.,* 2015), and require harmonious monitoring schemes. Furthermore, the conservation decisions and management actions are typically done on a national level, which is why these borders need to be taken into account although species do not recognize border lines (Pouzols *et al.,* 2014).

458 Unfortunately corresponding long-term census data from the border countries,
459 especially from the Russian side, are lacking. Furthermore, the alarming results show
460 that the former climatic conditions in the northwest corner of Finland have already
461 moved out of Finland at least on the 50-km grid scale. Although in this mountainous
462 region, in the short-term species could cope with climate change by shifting their
463 densities uphill, in the long-term their currently declining populations (Lehikoinen *et*
464 *al.,* 2014) may become extirpated from northwestern Europe (Huntley *et al.,* 2007;
465 Virkkala *et al.,* 2008). This underlines that international collaboration should be
466 increased to improve our understanding of species abundance and distribution
467 changes (Jiguet *et al.,* 2010; Lehikoinen *et al.,* 2014) and to design management
468 actions to conserve biodiversity in the face of changing climate (Pearce-Higgins &
469 Green, 2014; Pouzols *et al.,* 2014).
470
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472
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479
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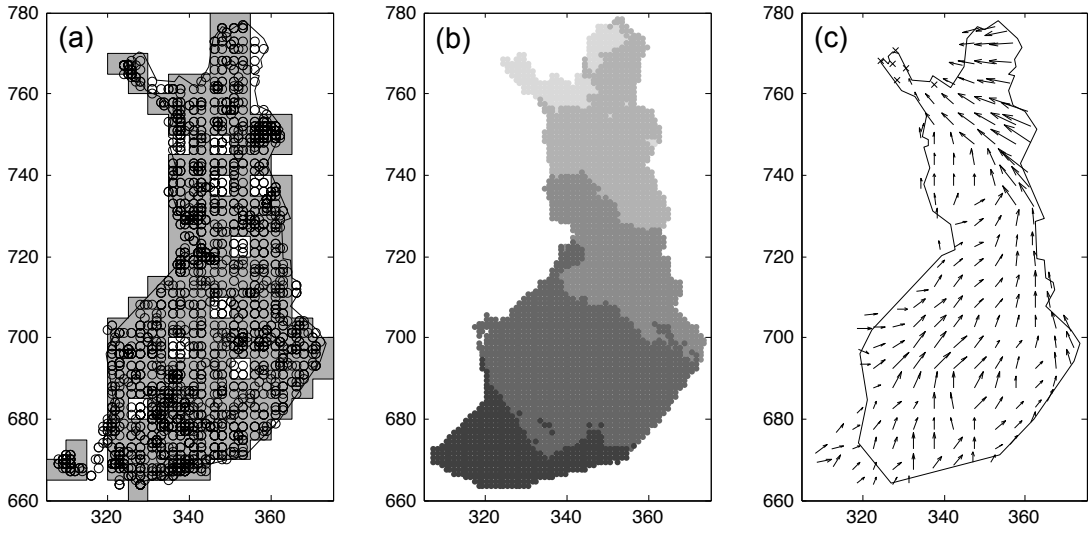

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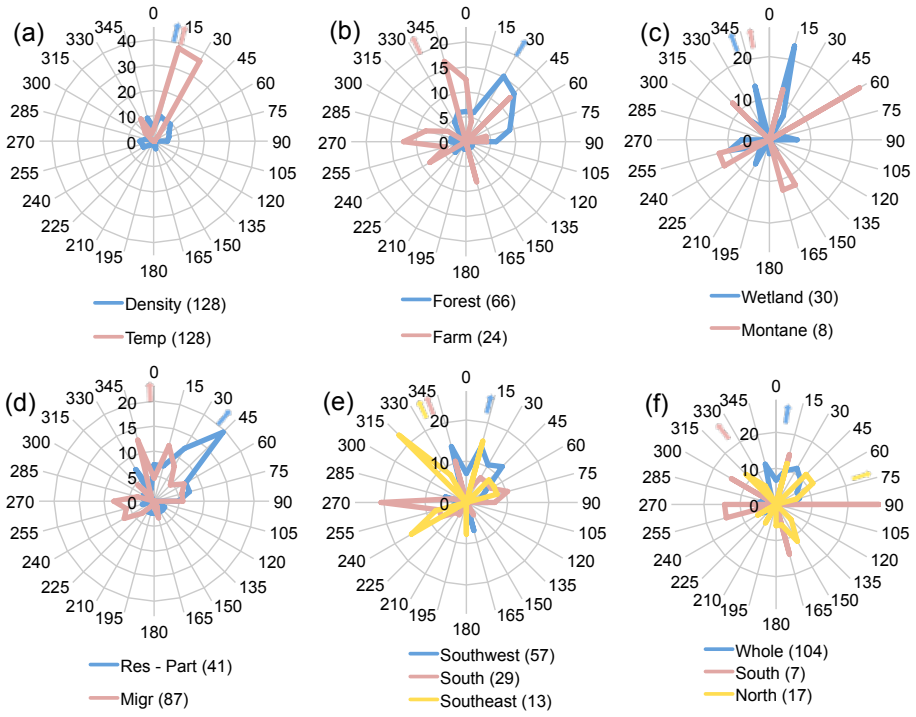
636 Fig. 1. Map of Finland showing a) 50-km grid cells in grey and individual census sites

637 in circles in the 1970s, 1980s and 2000s, b) isoterms in annual temperature during

638 1970–1989 (darker colour indicate warmer tempeature) and c) directions that

639 temperature has changed in Finland between 1970–1989 and 2000–2012. Longer
640 arrows indicate stronger temperature shifts. ‘x’-marks show grids where climate in the
641 1970s and 1980s no longer exists in Finland during the second study period.
642



643

644 Fig. 2. Distribution of directions of density shifts. (a) Densities of all species (95% c.
645 i. of the mean direction 358–30°) and corresponding temperature (95 % c. i. 8–17°) in
646 their same breeding range from 1970–1989 to 2000–2012. Distribution of directions
647 of density shifts according to main habitat type of the species [b) farmland and forest
648 species and c) wetland and montane species], migration behaviour [d) residents -
649 partial migrants and fully migratory species], spring migration direction [e) southwest,
650 south or southeast] and general distribution of the species [f) southern edge, large part
651 of the country and northern edge]. The colour lines show the distribution of directions
652 in 15° intervals and the colour arrows next to the degrees show the mean direction of
653 the particular distribution.
654

655 Supporting information

656

657 Supplementary Table 1. Species-specific data with sample sizes, habitat, migration
658 and distribution classifications, central gravity of density expressed as latitudes and
659 longitudes during both study periods, direction of the density shift, total distance of
660 shift density shift along latitude and longitude directions and direction of the species-
661 specific temperature shift.

662

663 Supplementary Figs. 1–128. Species-specific density maps during the first (1970-
664 1989, left panel) and second (2000-2012, right panel) study period.

665

666 Supplementary Fig. 129. Illustration of moved densities of species to estimate the
667 potential effect of shape of the country on the direction of density shifts.

668

669 Supplementary Fig. 130. Grid specific changes of relative densities of groups of
670 species classified based on their main habitat type.

671

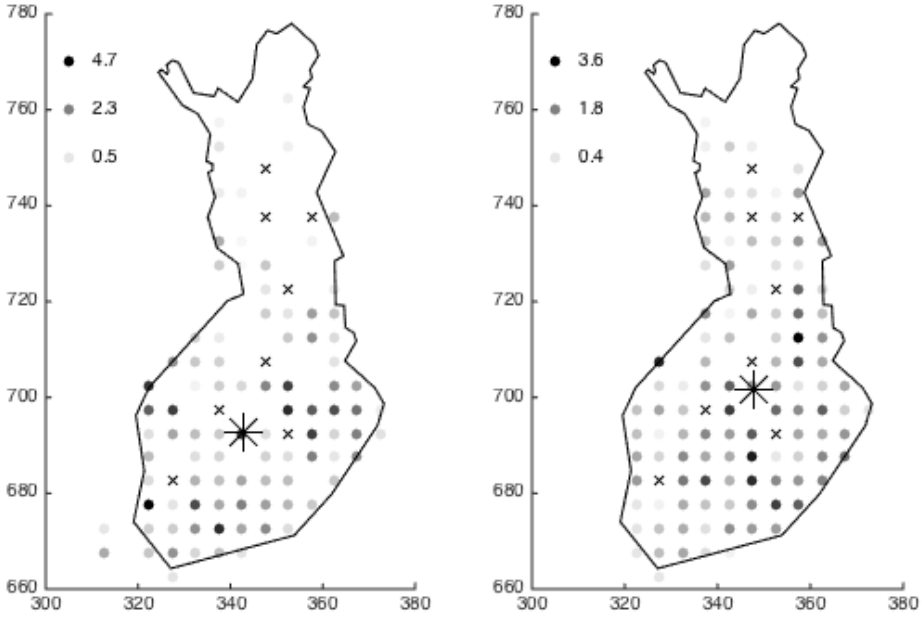
672 Supplementary Fig. 131. Grid specific changes of relative densities of groups of
673 species classified based on their migration type.

674

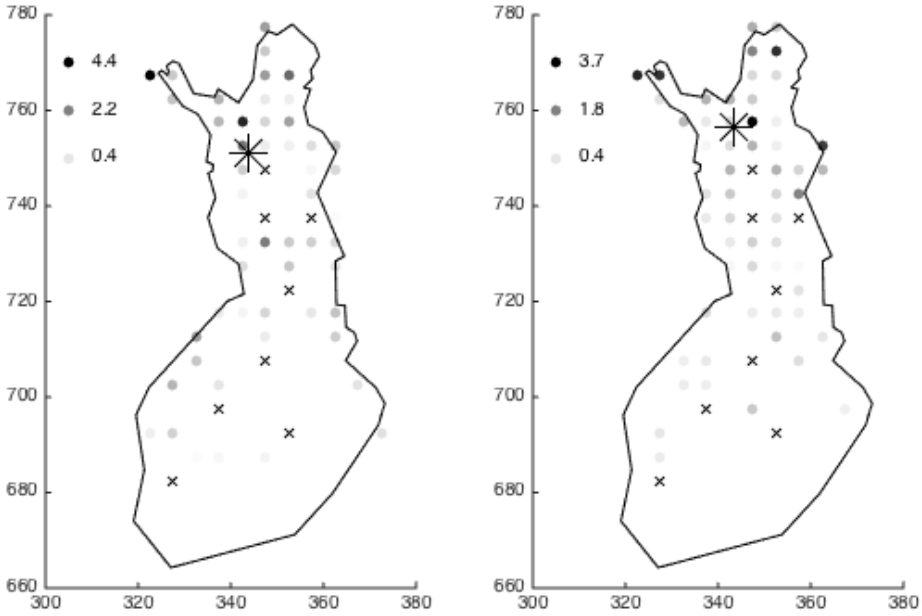
675 Supplementary Fig. 132. Distribution of directions of changes in densities based on
676 four migration groups.

677

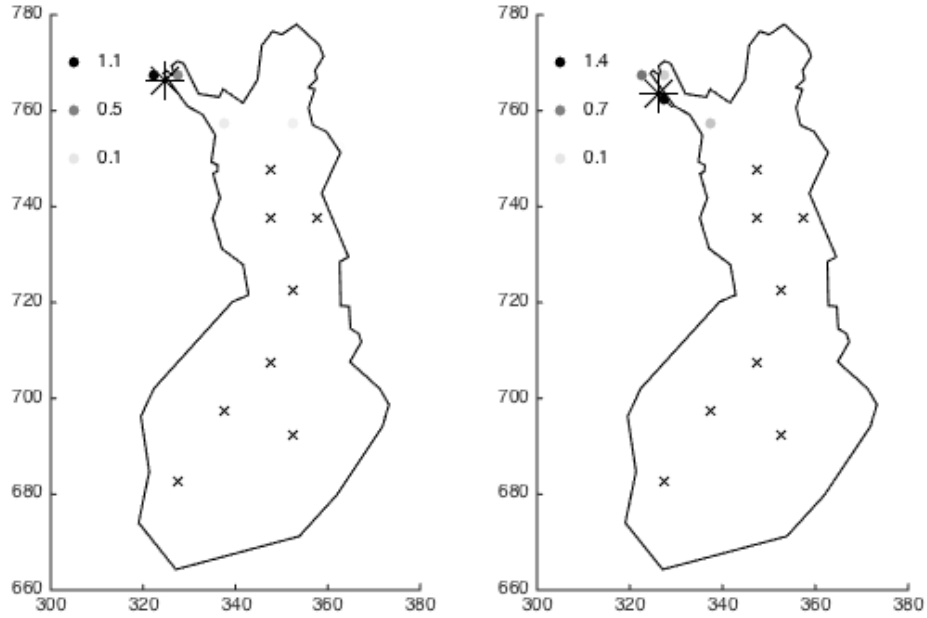
Supplementary figs 1–128. Species-specific density maps during the first (1970-1989, left panel) and second (2000-2012, right panel) study period. The 50-km grid-specific densities are shown in grey scale illustrated by three values on the up left corned or each panel. Large asterisk shows the central gravity of the densities and small black crosses are grids that did not have enough data (excluded from the analyses).



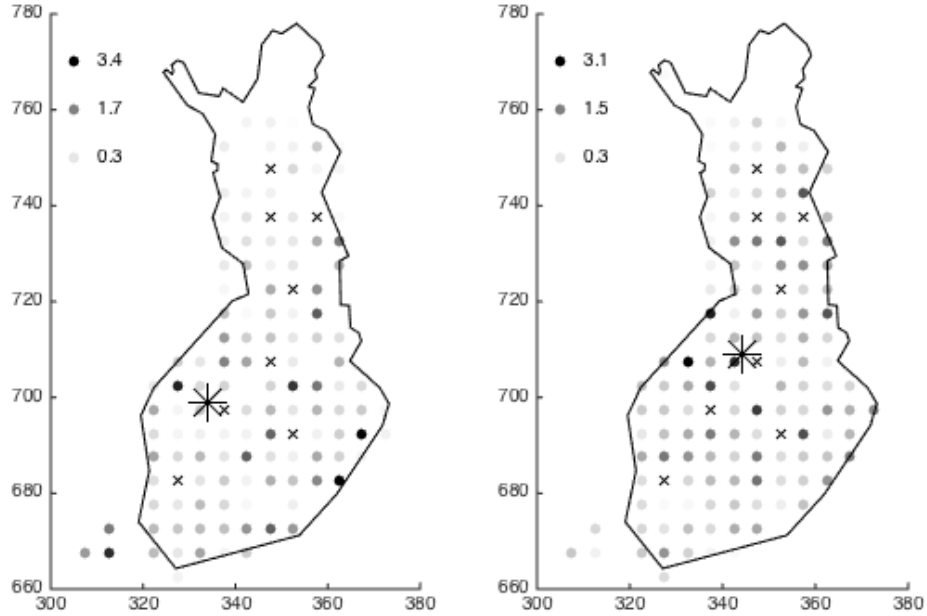
Supplementary fig. 1. Tetrastes bonasia



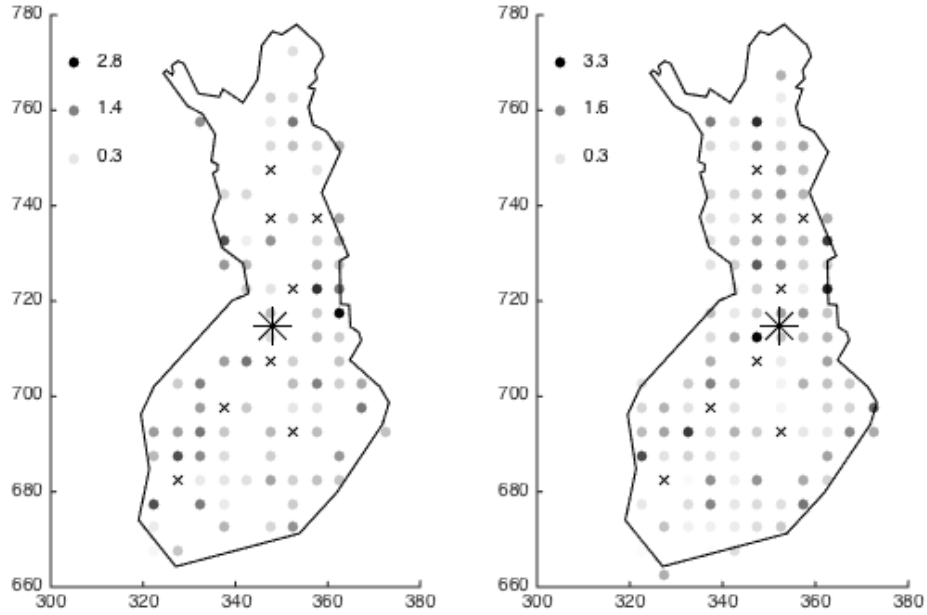
Supplementary fig. 2. Lagopus lagopus



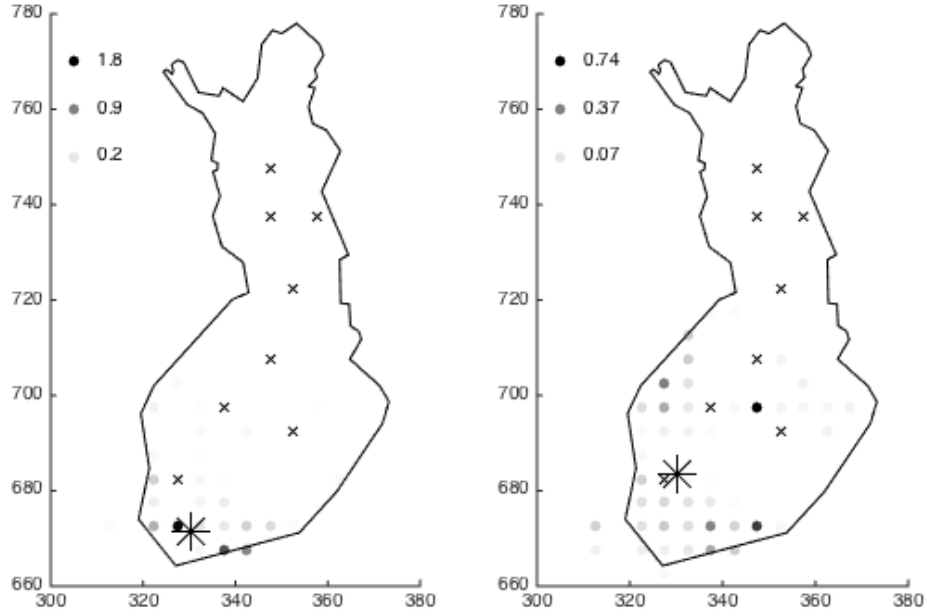
Supplementary fig. 3. Lagopus muta



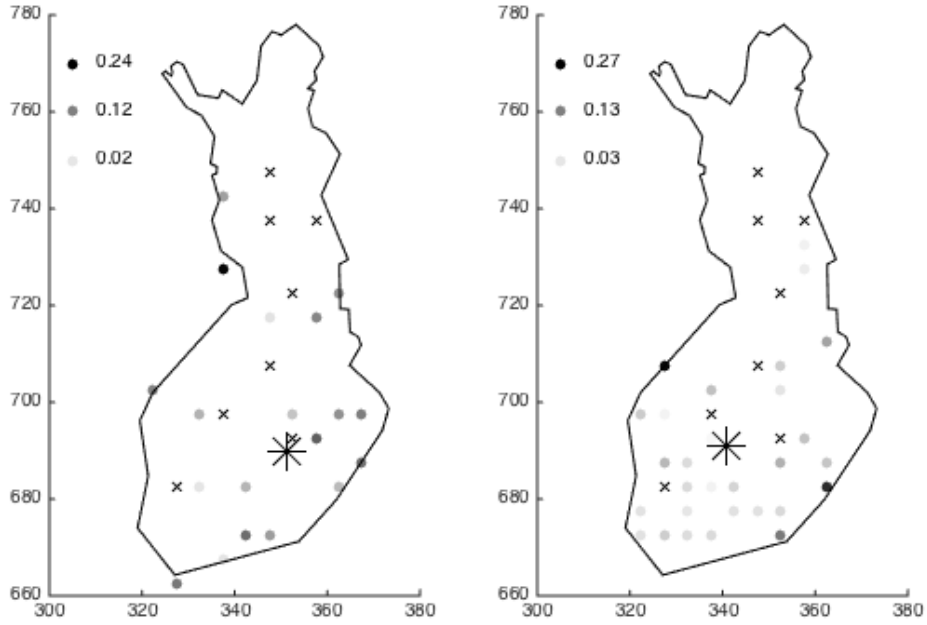
Supplementary fig. 4. Tetrao tetrix



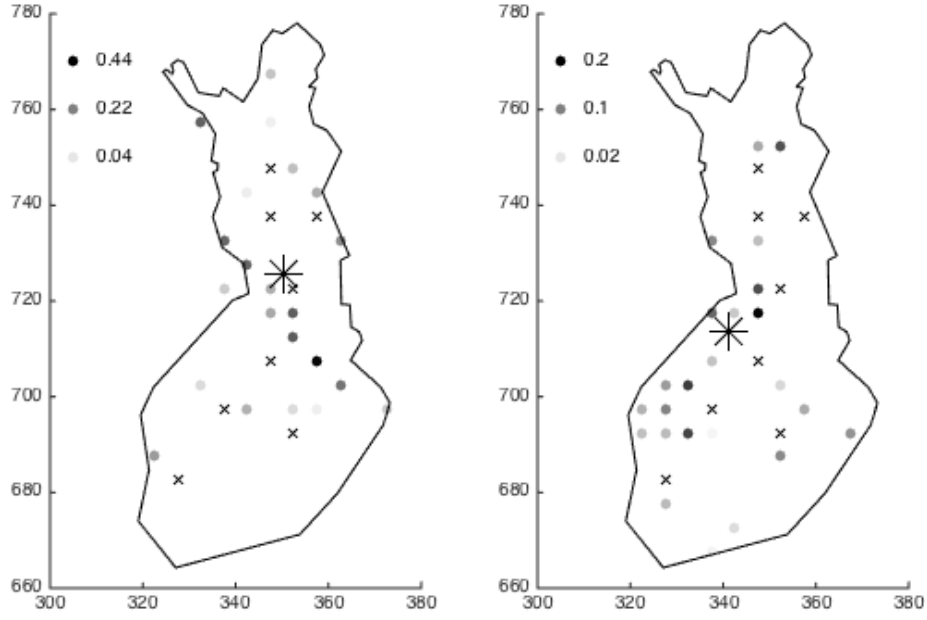
Supplementary fig. 5. Tetrao urogallus



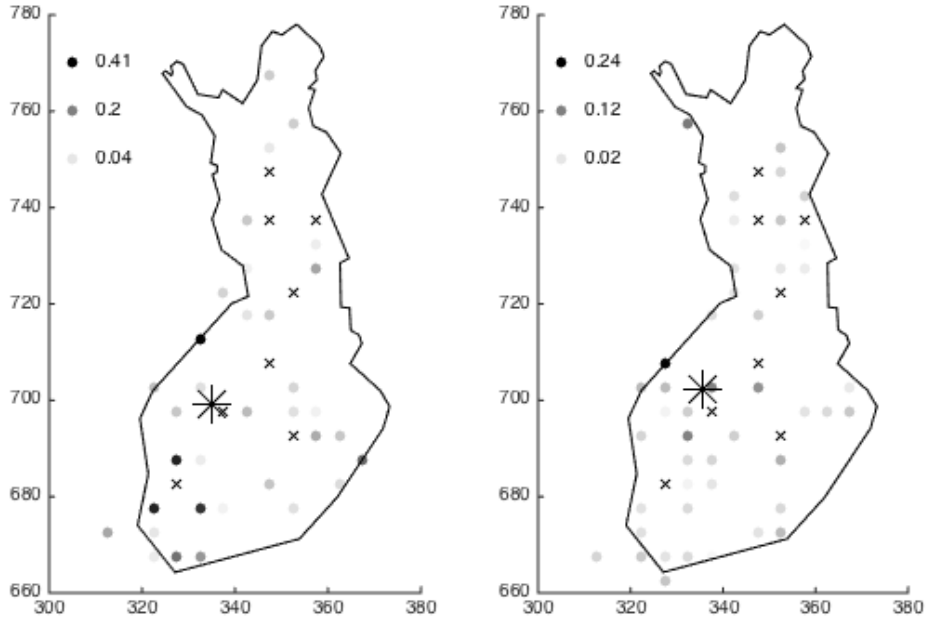
Supplementary fig. 6. Phasianus colchicus



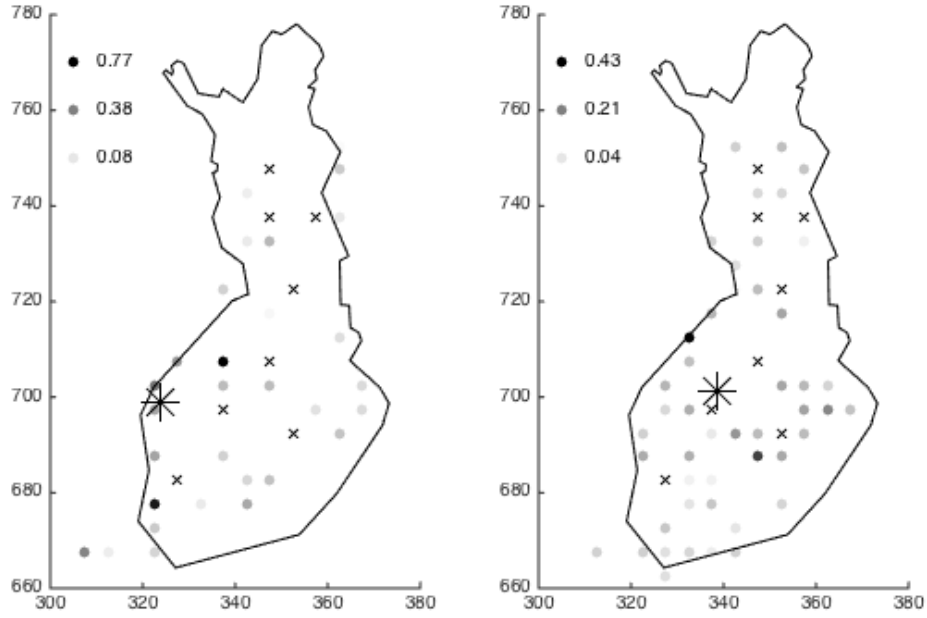
Supplementary fig. 7. Pernis apivorus



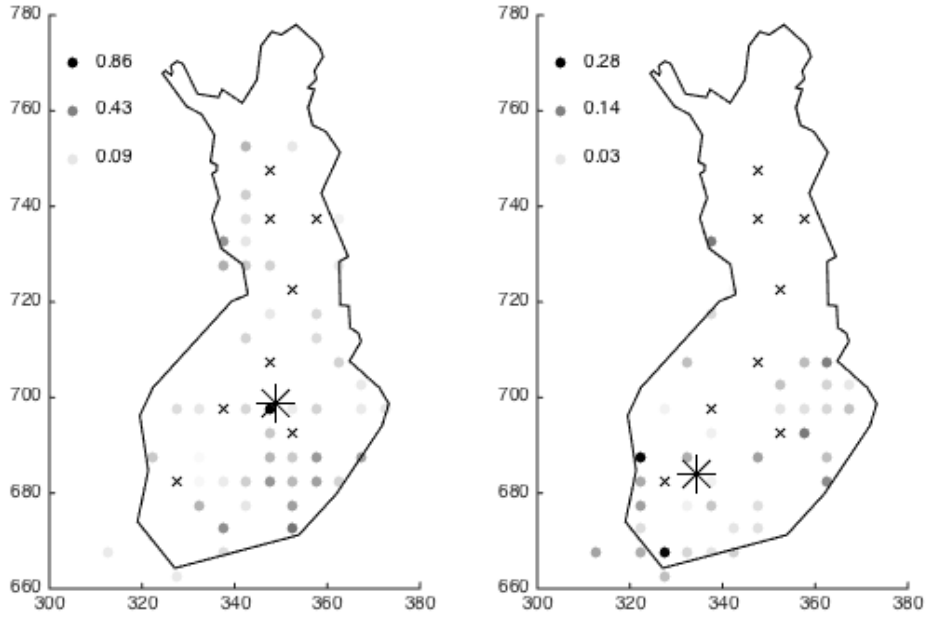
Supplementary fig. 8. Circus cyaneus



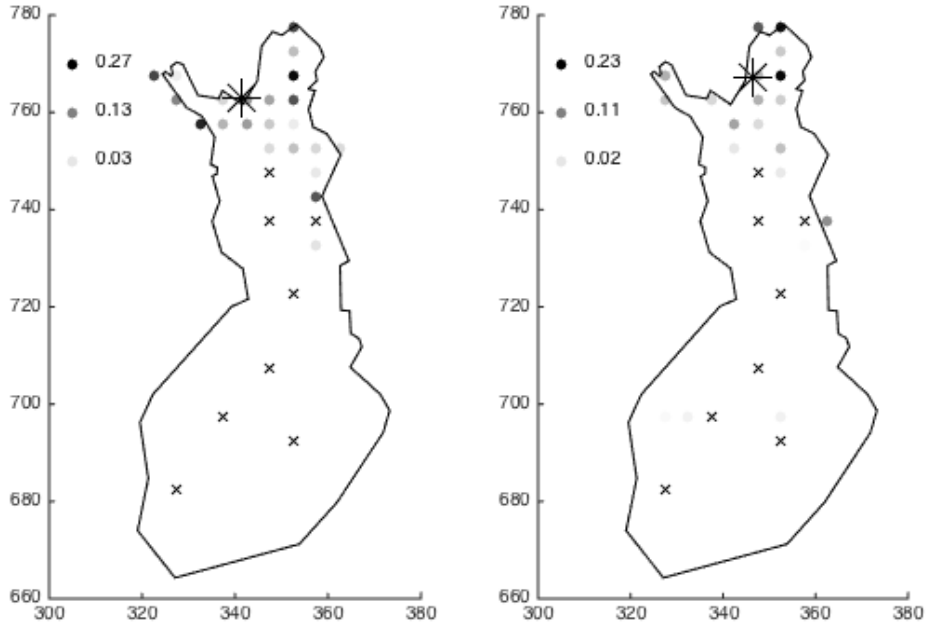
Supplementary fig. 9. Accipiter gentilis



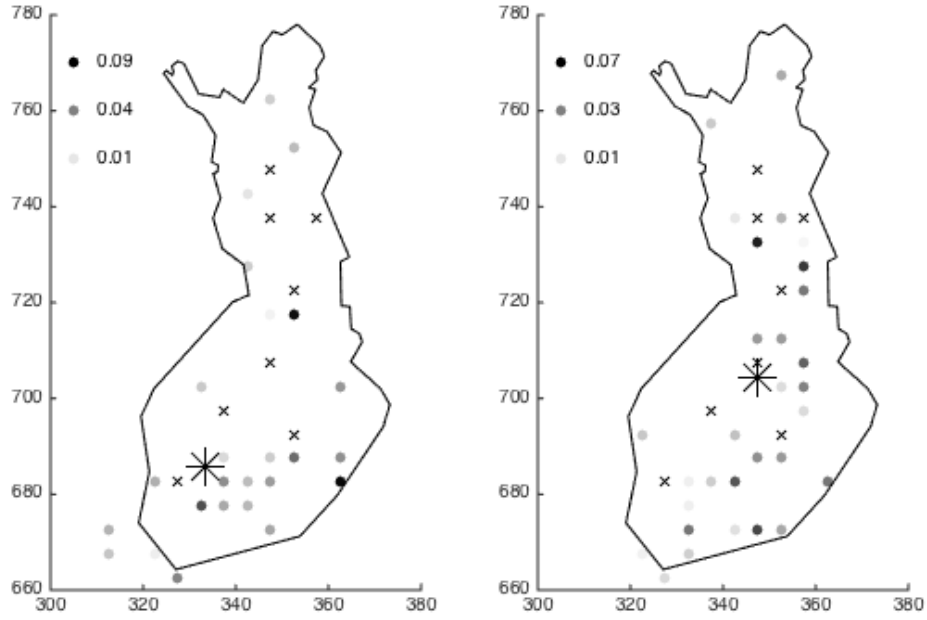
Supplementary fig. 10. Accipiter nisus



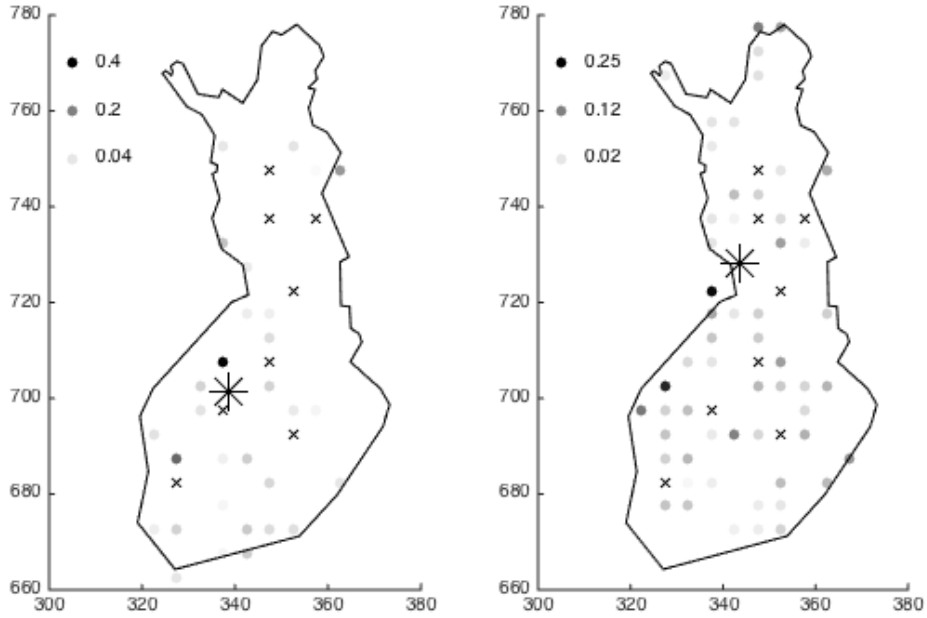
Supplementary fig. 11. Buteo buteo



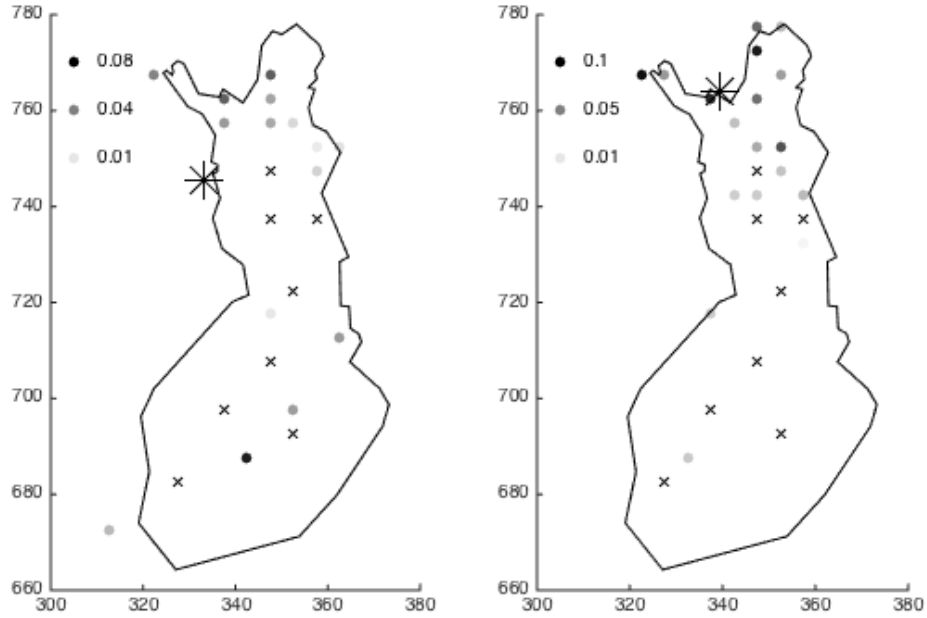
Supplementary fig. 12. Buteo lagopus



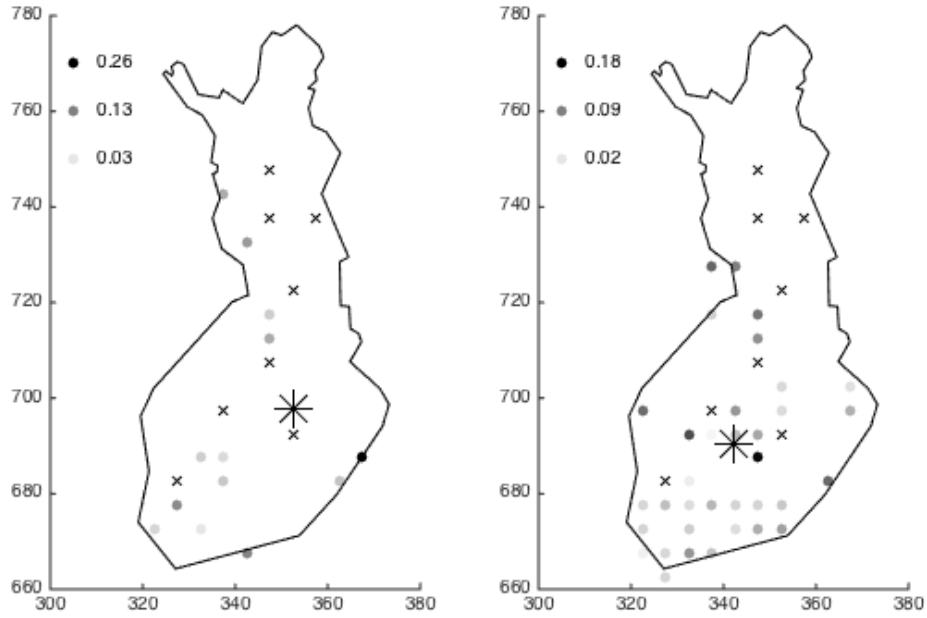
Supplementary fig. 13. Pandion haliaetus



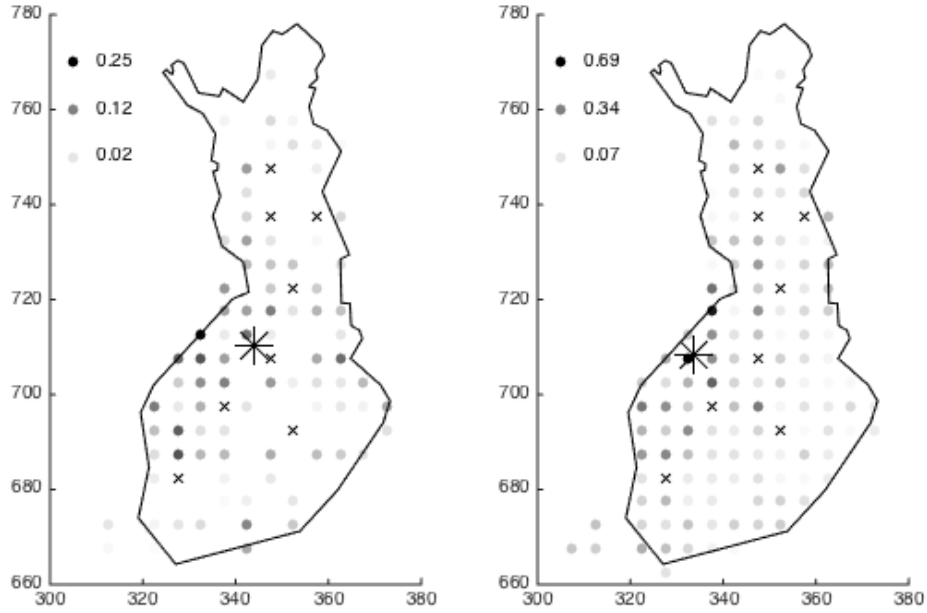
Supplementary fig. 14. Falco tinnunculus



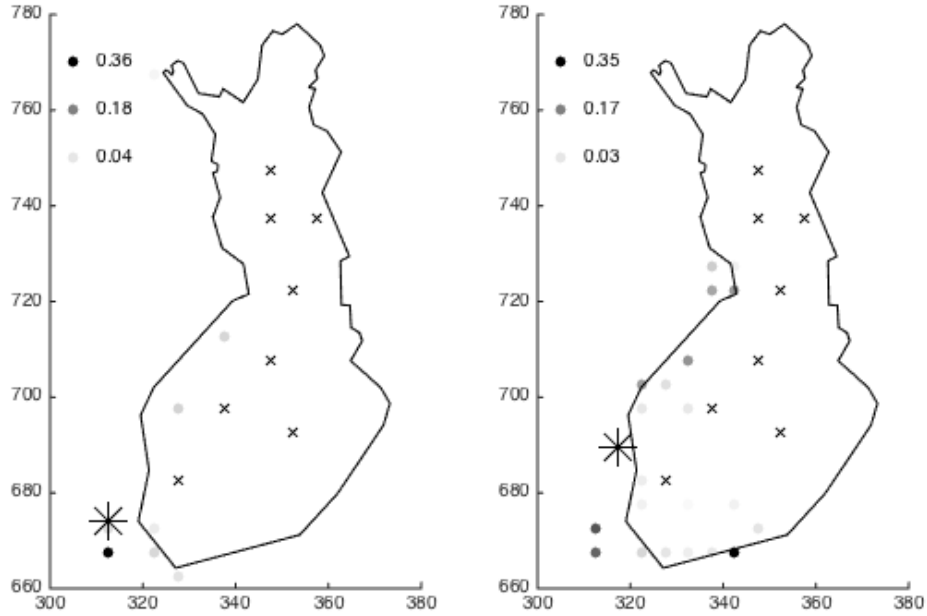
Supplementary fig. 15. Falco columbarius



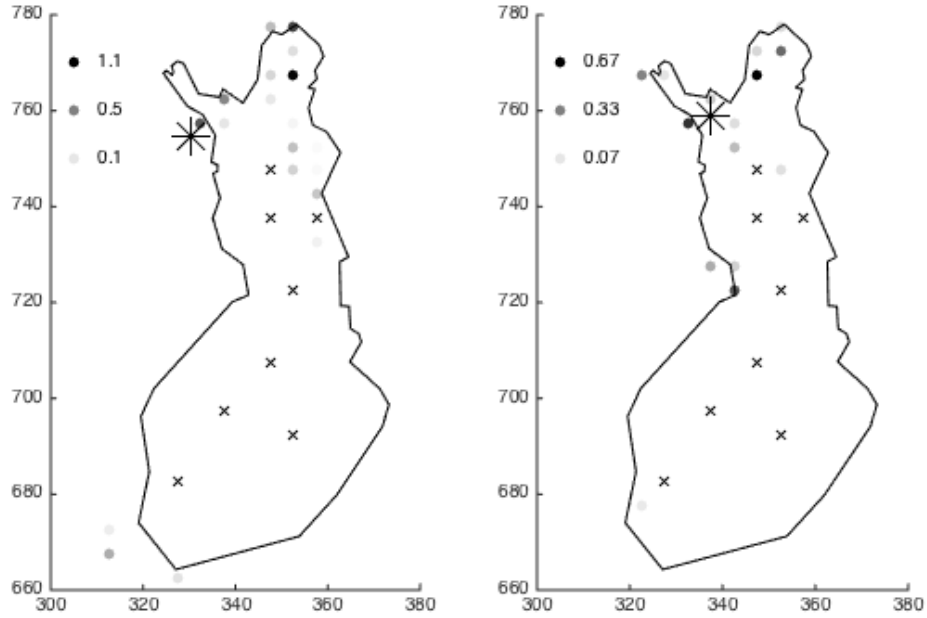
Supplementary fig. 16. Falco subbuteo



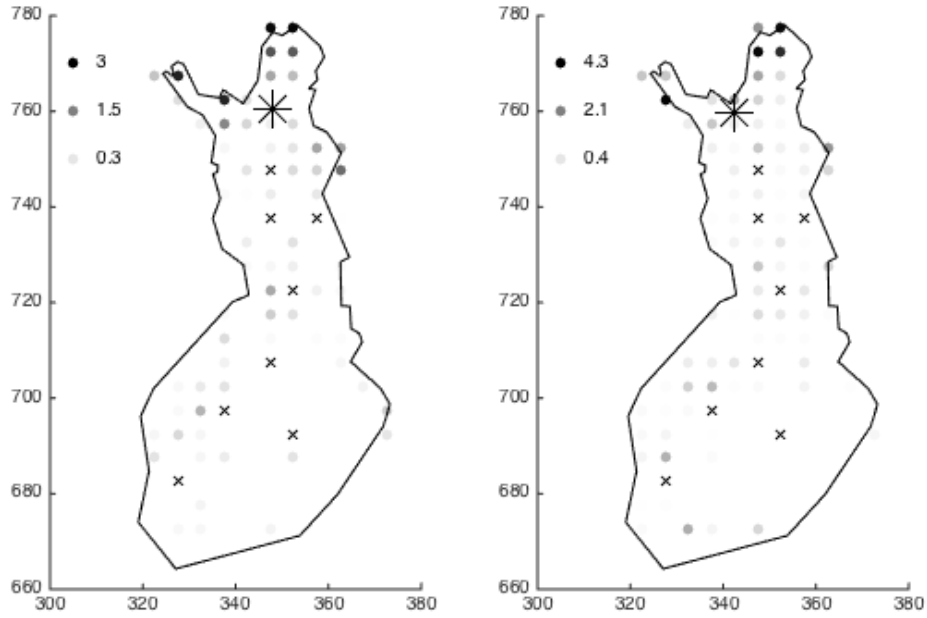
Supplementary fig. 17. Grus grus



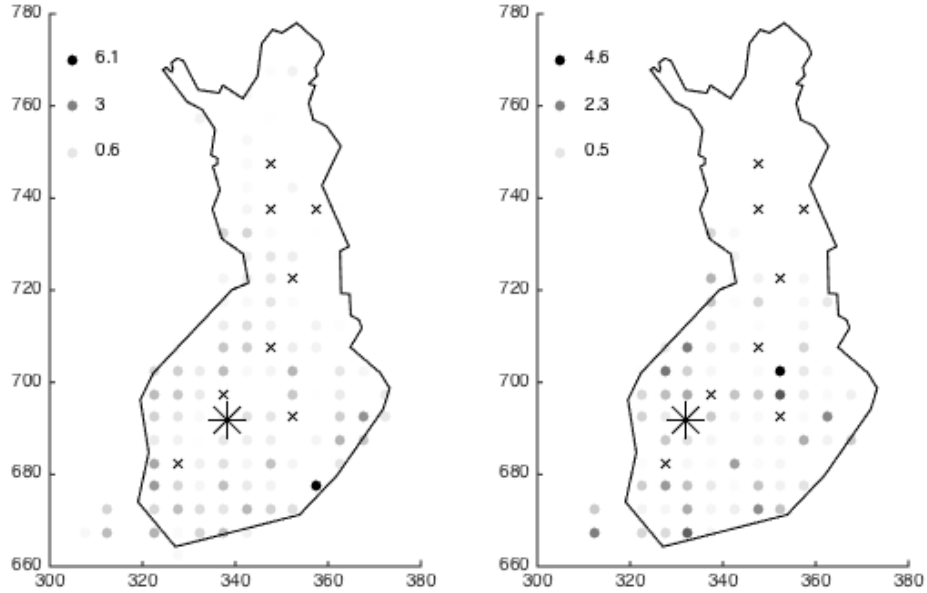
Supplementary fig. 18. Haematopus ostralegus



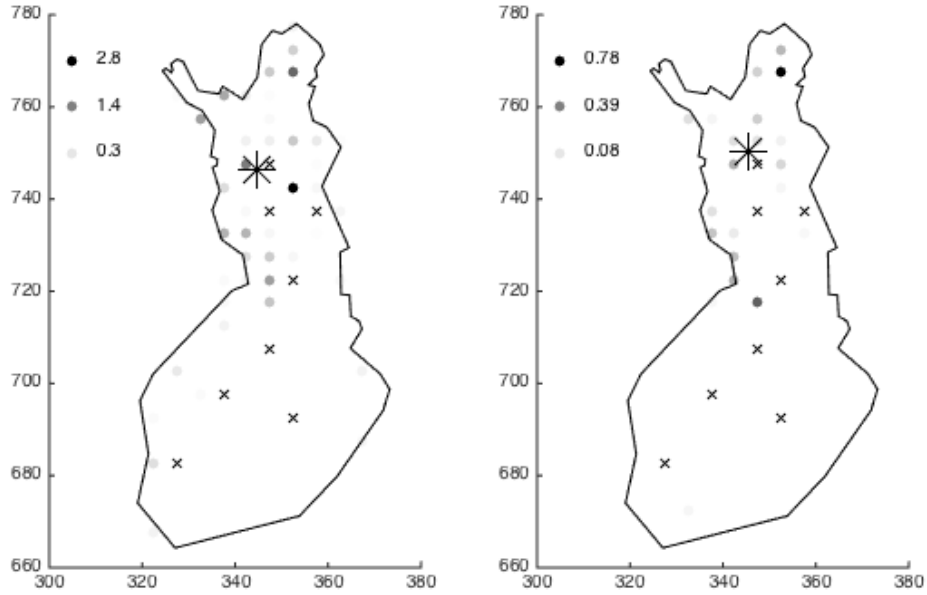
Supplementary fig. 19. Charadrius hiaticula



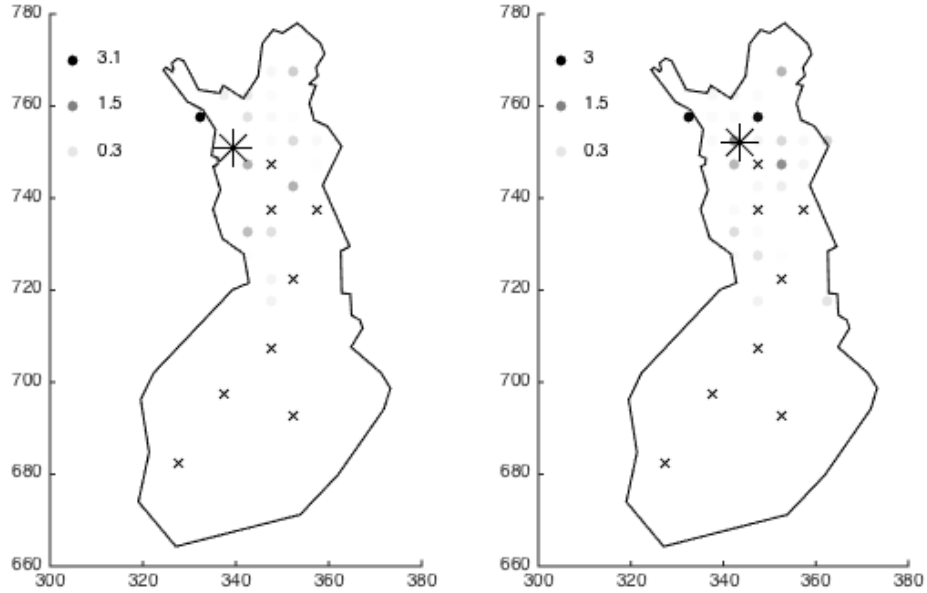
Supplementary fig. 20. Pluvialis apricaria



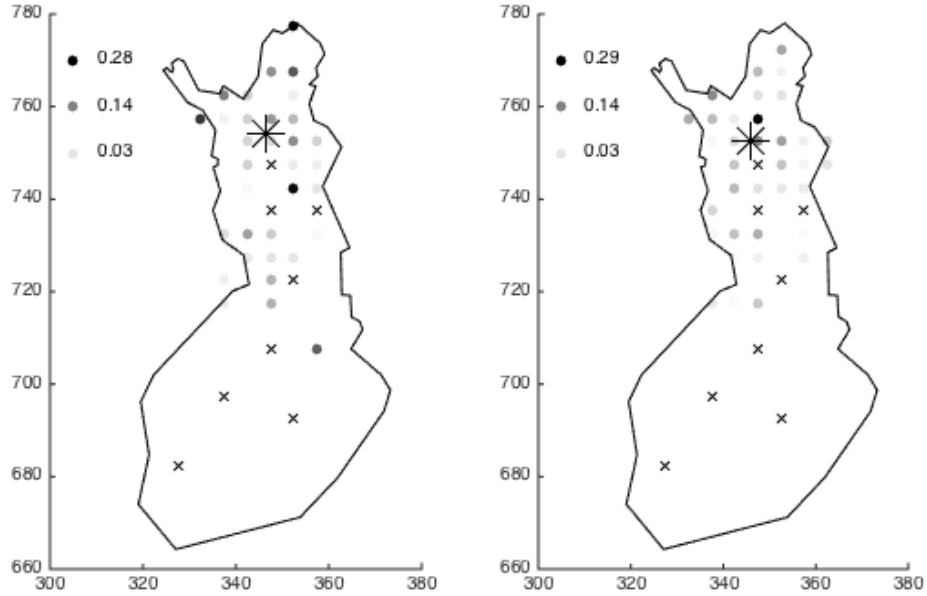
Supplementary fig. 21. Vanellus vanellus



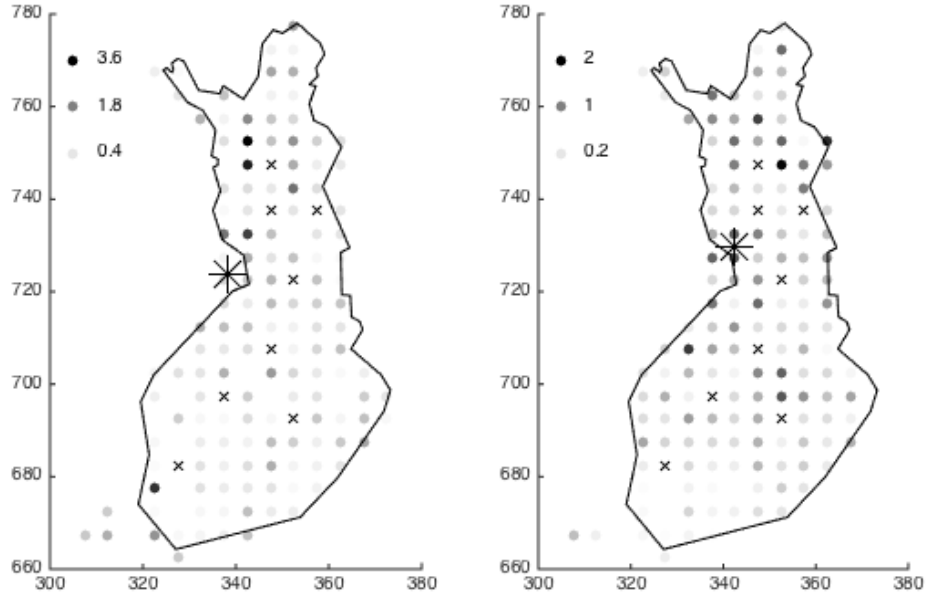
Supplementary fig. 22. Calidris pugnax



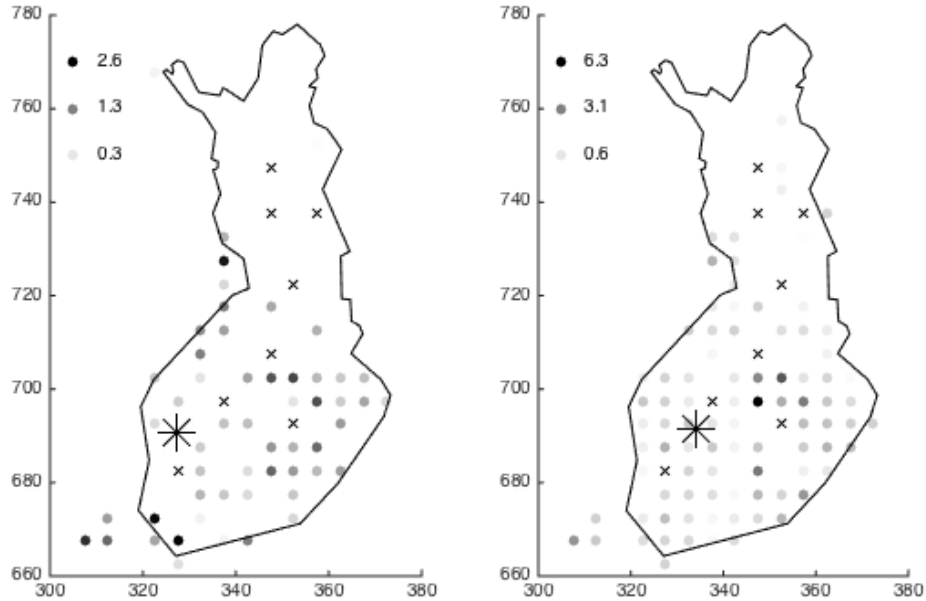
Supplementary fig. 23. Calidris falcinellus



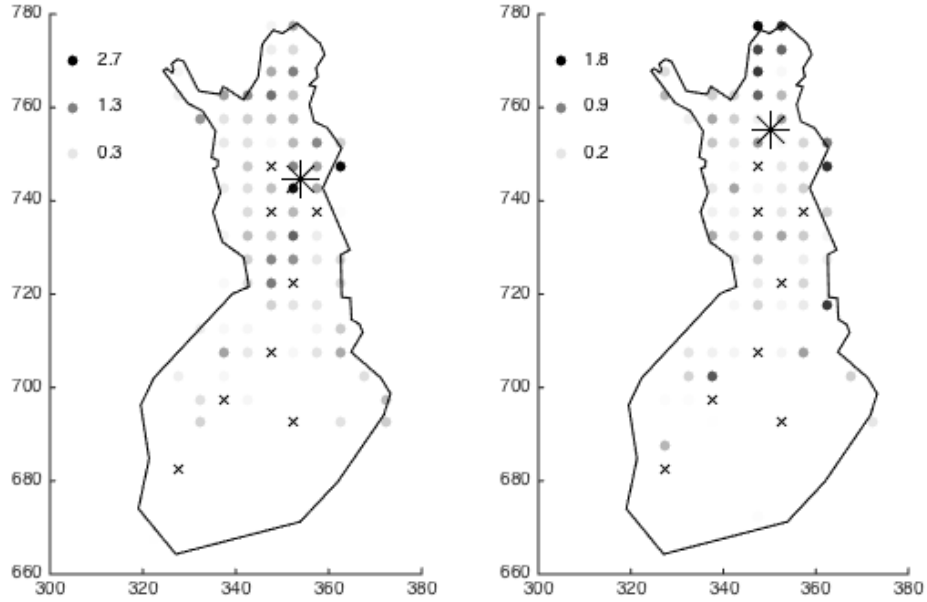
Supplementary fig. 24. Lymnocryptes minumus



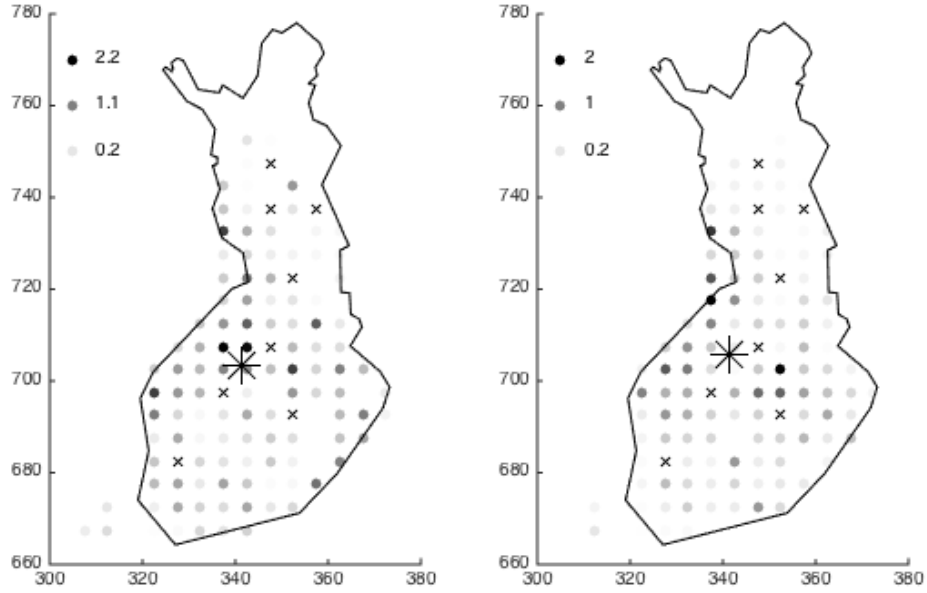
Supplementary fig. 25. Gallinago gallinago



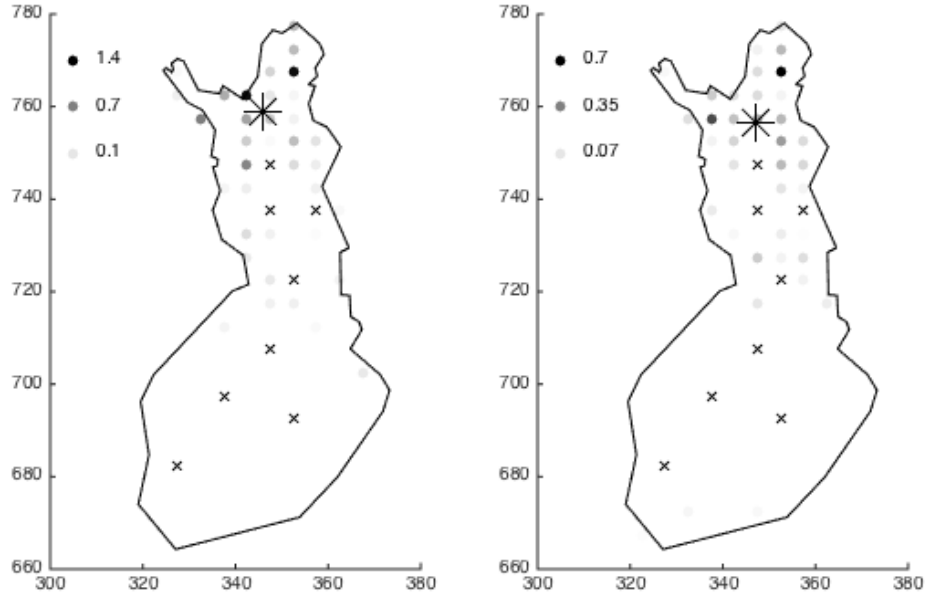
Supplementary fig. 26. Scolopax rusticola



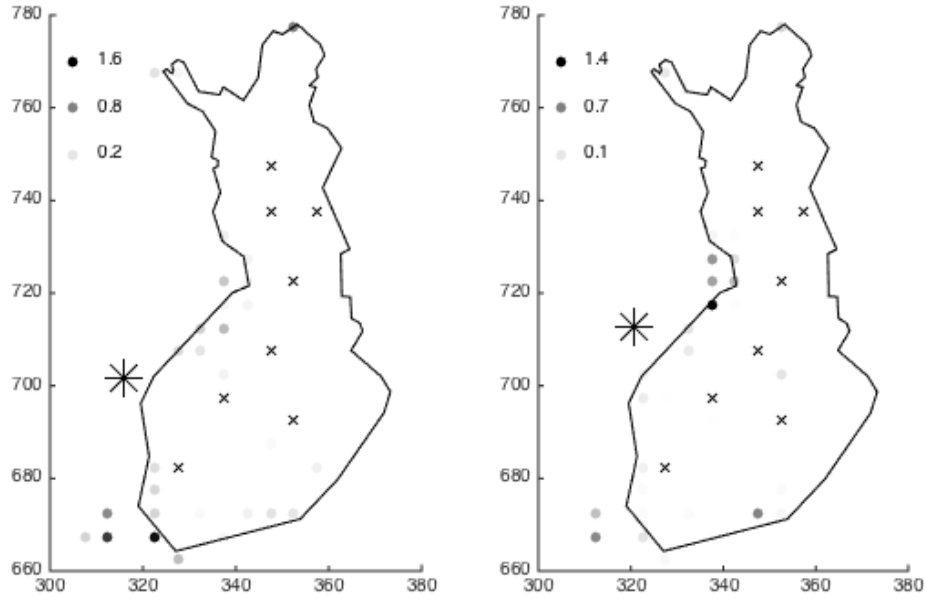
Supplementary fig. 27. Numenius phaeopus



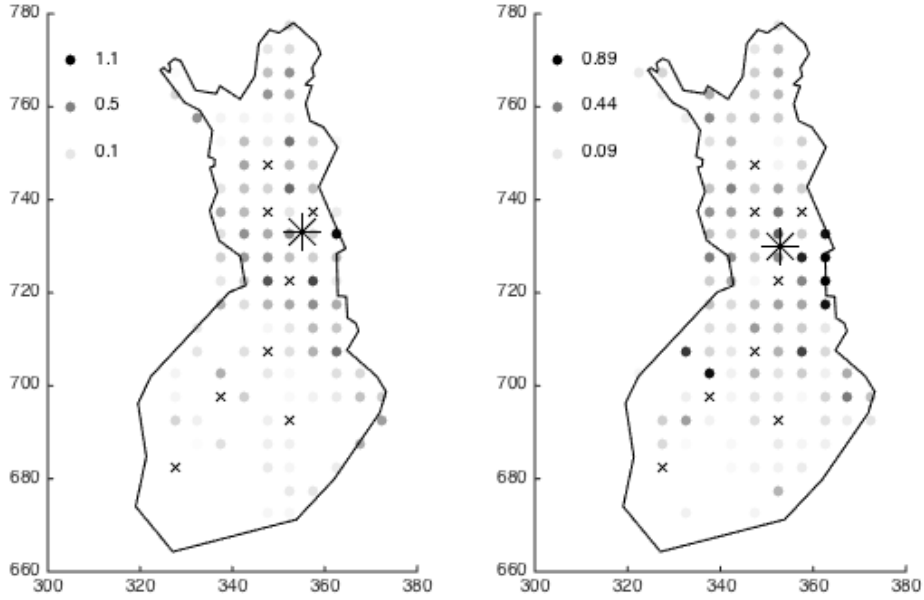
Supplementary fig. 28. Numenius arquata



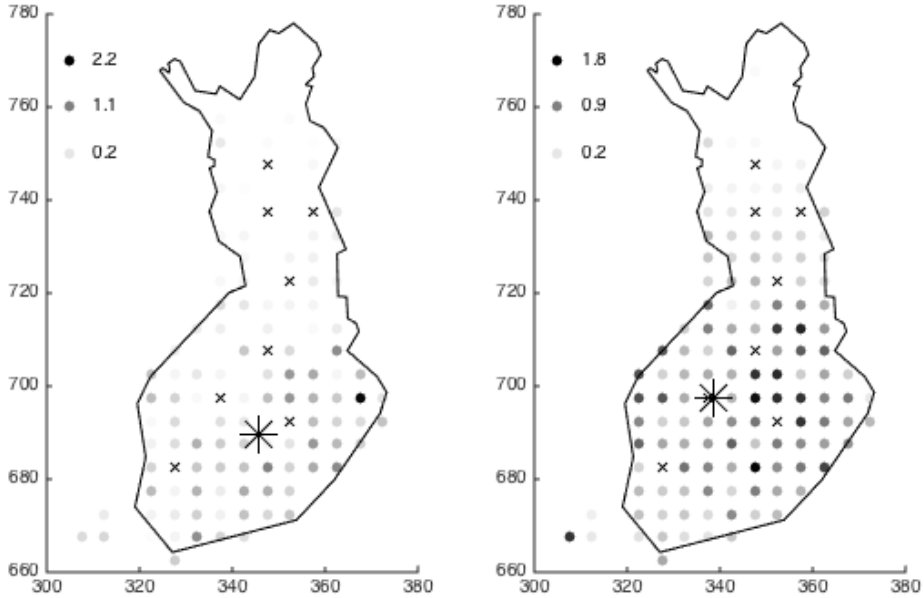
Supplementary fig. 29. Tringa erythropus



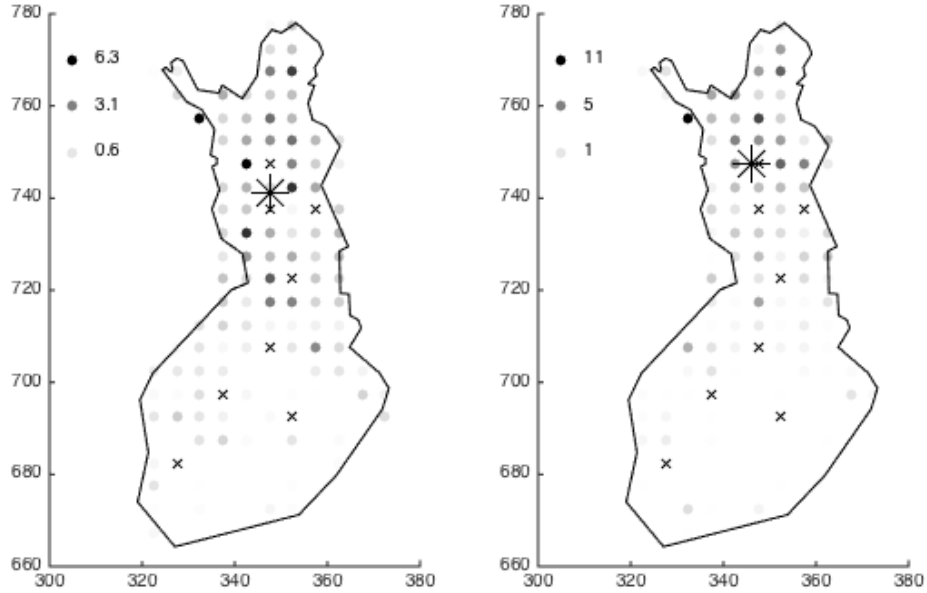
Supplementary fig. 30. Tringa totanus



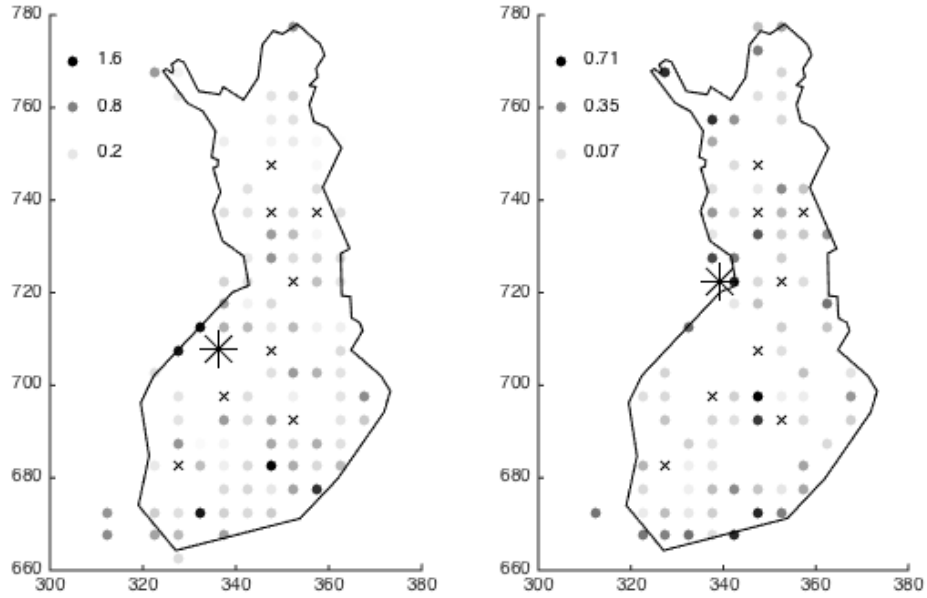
Supplementary fig. 31. Tringa nebularia



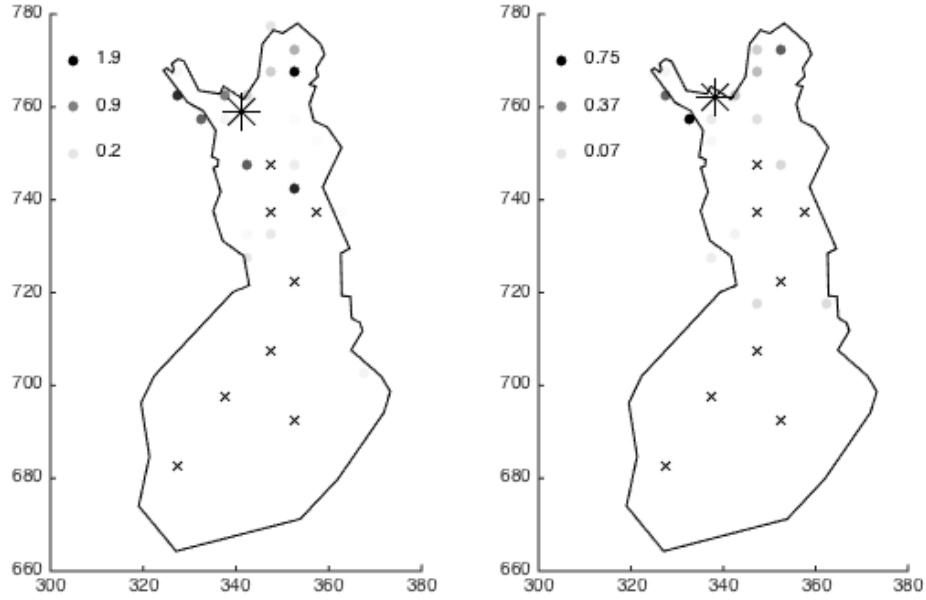
Supplementary fig. 32. Tringa ochropus



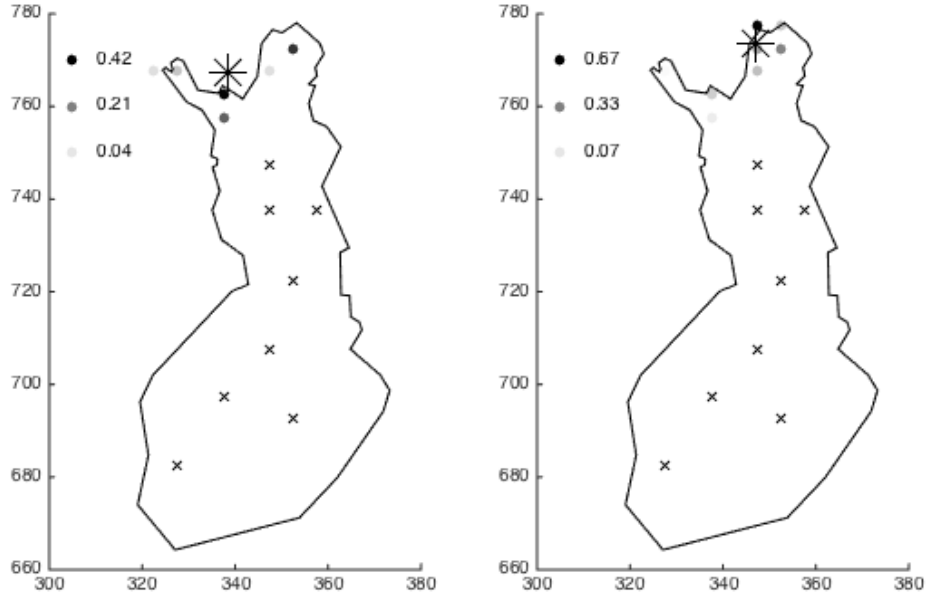
Supplementary fig. 33. Tringa glareola



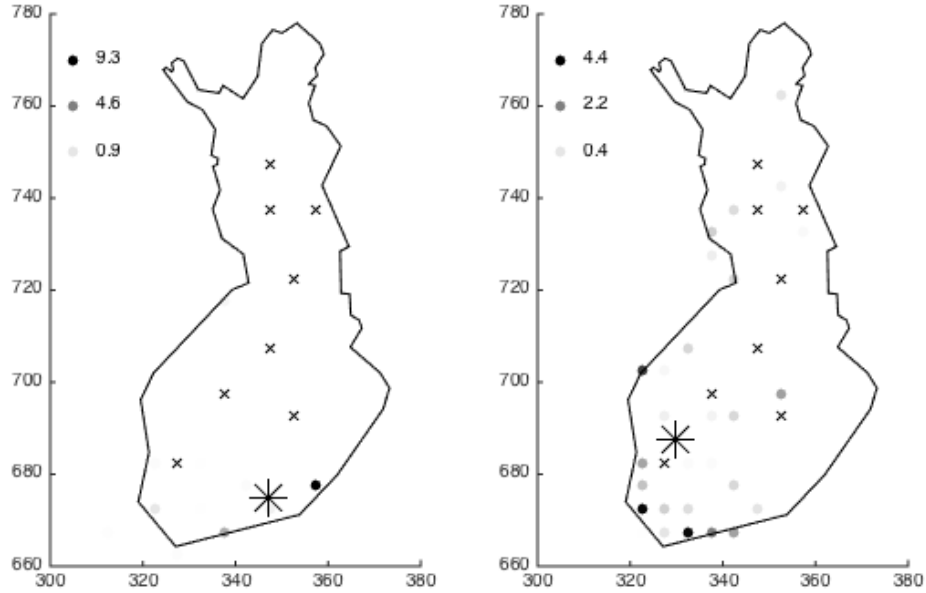
Supplementary fig. 34. Actitis hypoleucos



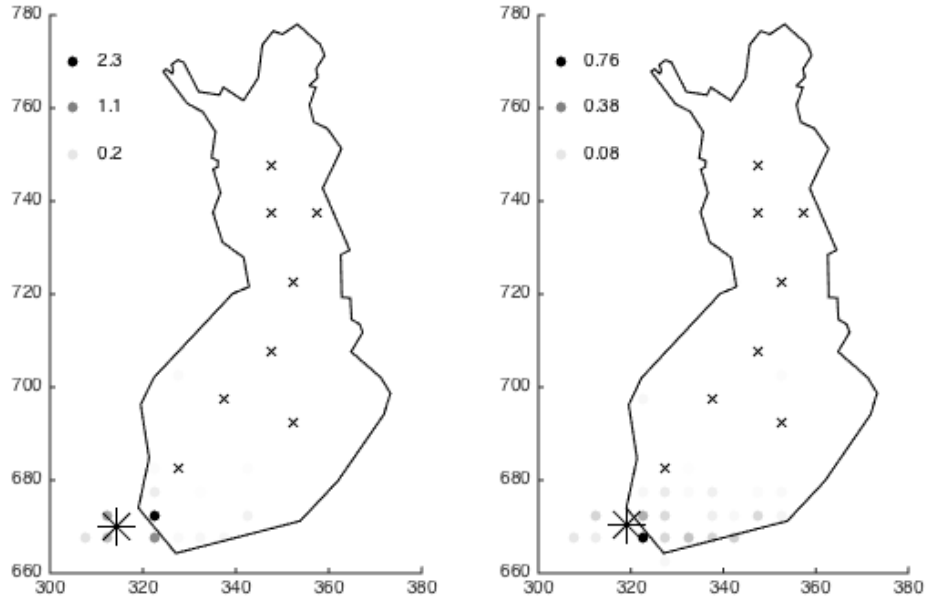
Supplementary fig. 35. Phalaropus lobatus



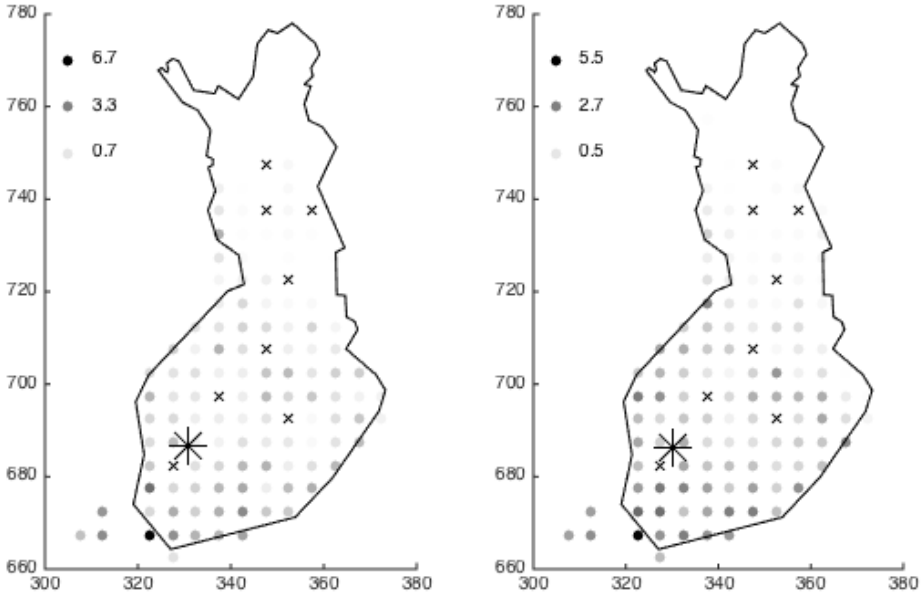
Supplementary fig. 36. Stercorarius longicaudus



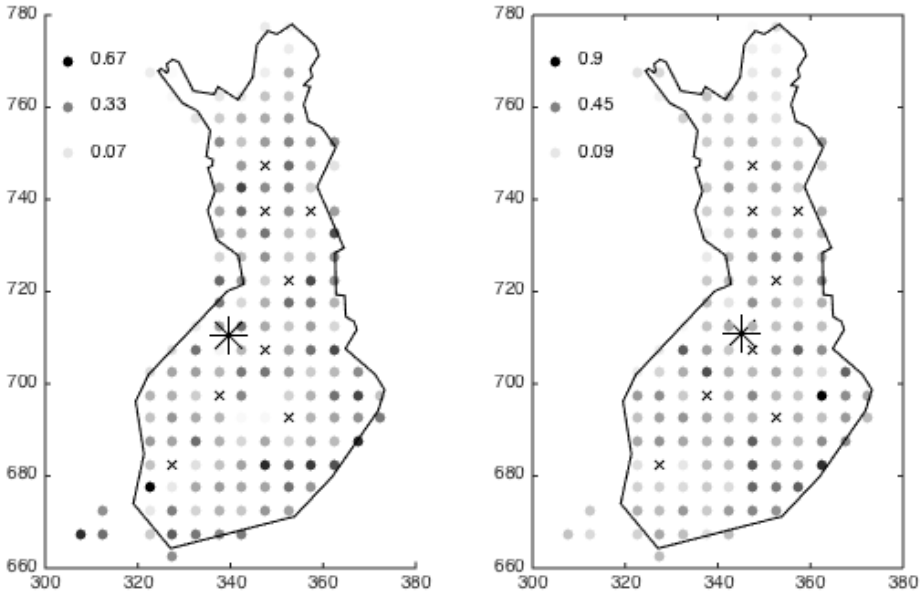
Supplementary fig. 37. Columba livia



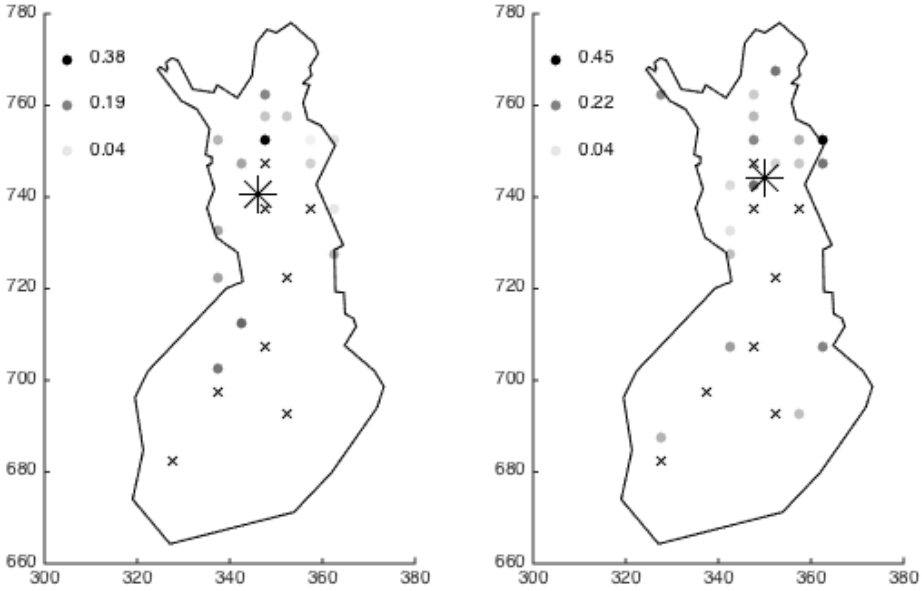
Supplementary fig. 38. Columba oenas



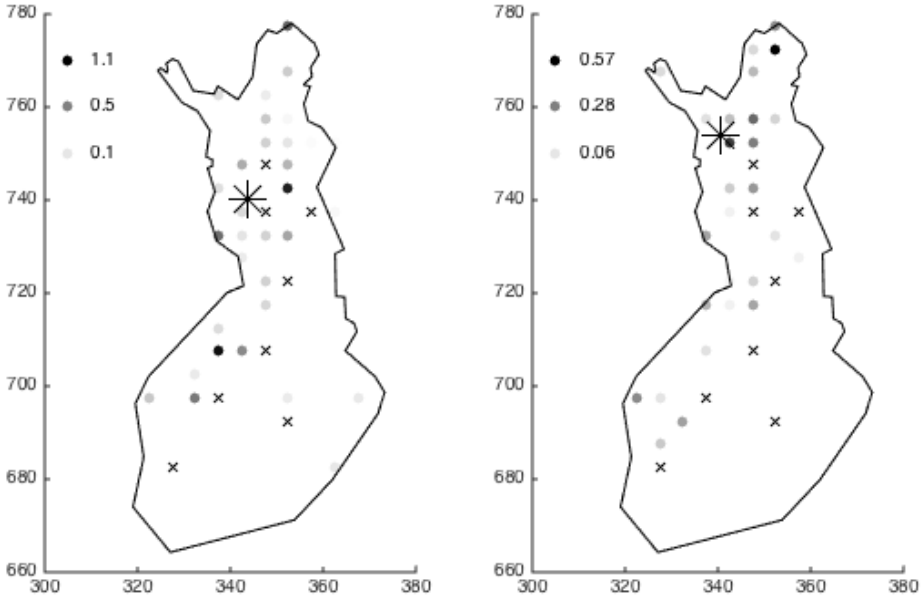
Supplementary fig. 39. Columba palumbus



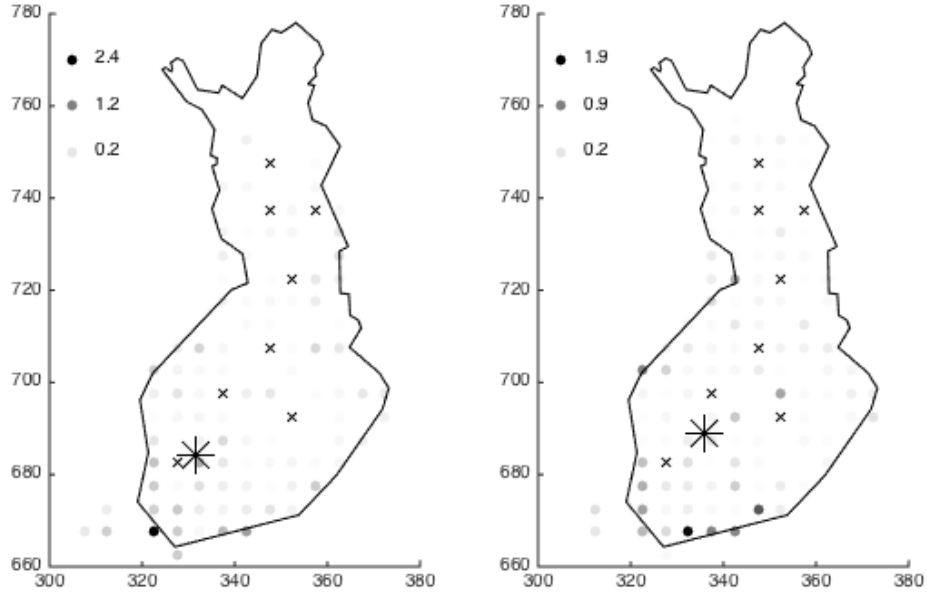
Supplementary fig. 40. Cuculus canorus



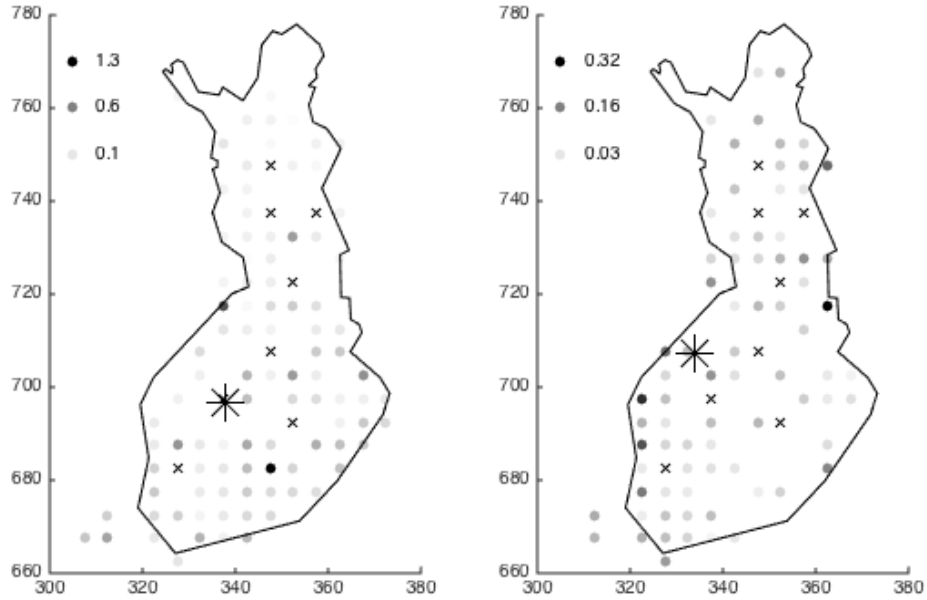
Supplementary fig. 41. Surnia ulula



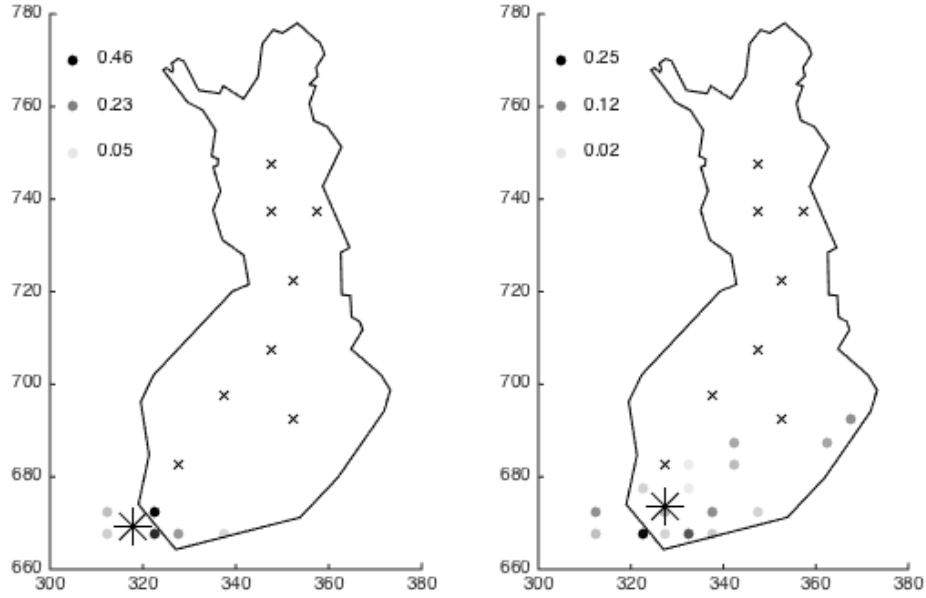
Supplementary fig. 42. Asio flammeus



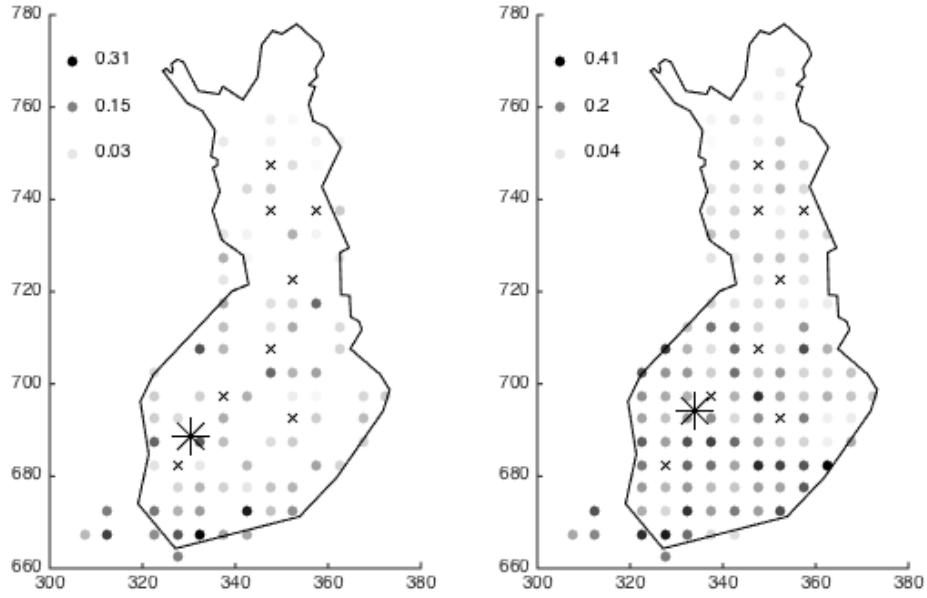
Supplementary fig. 43. Apus apus



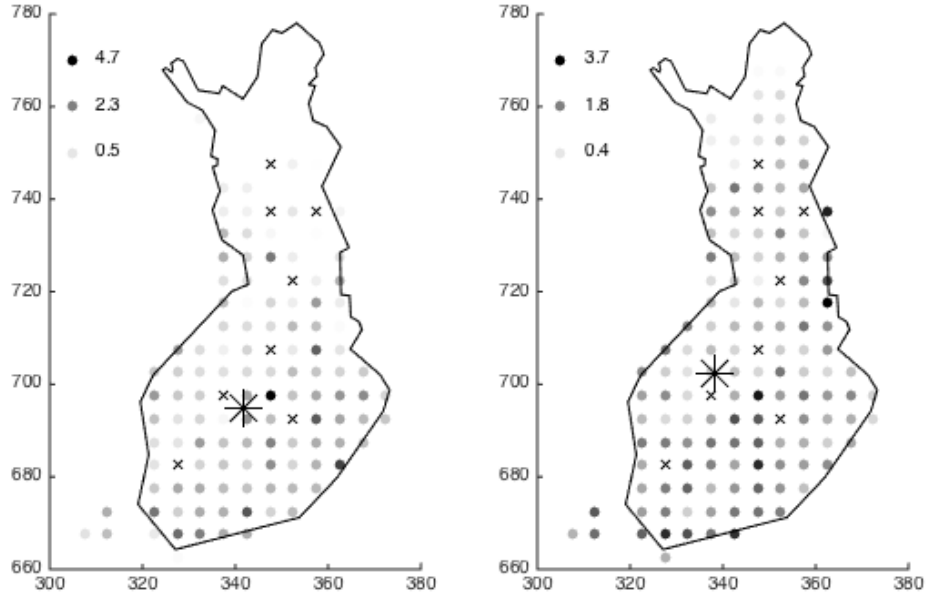
Supplementary fig. 44. Jynx torquilla



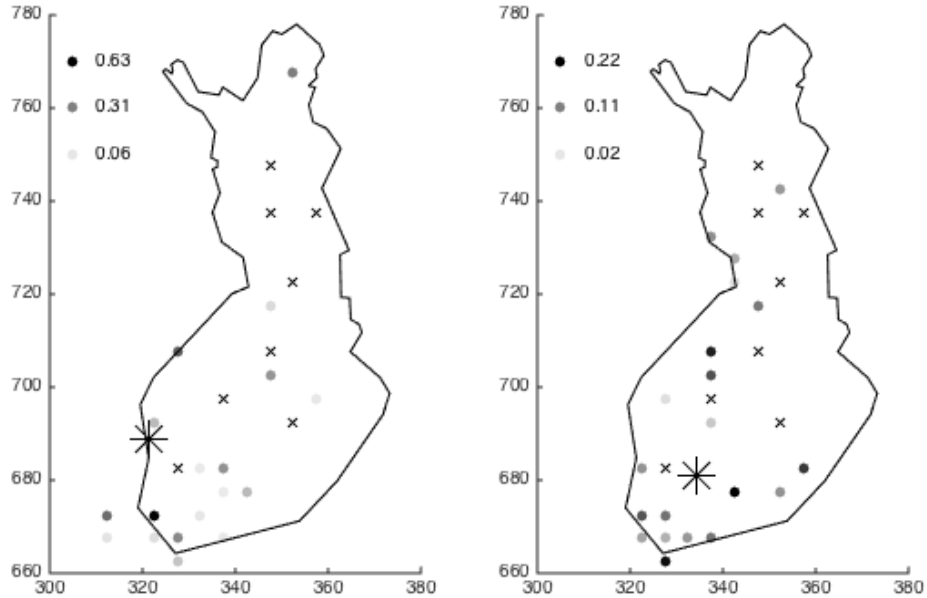
Supplementary fig. 45. Picus canus



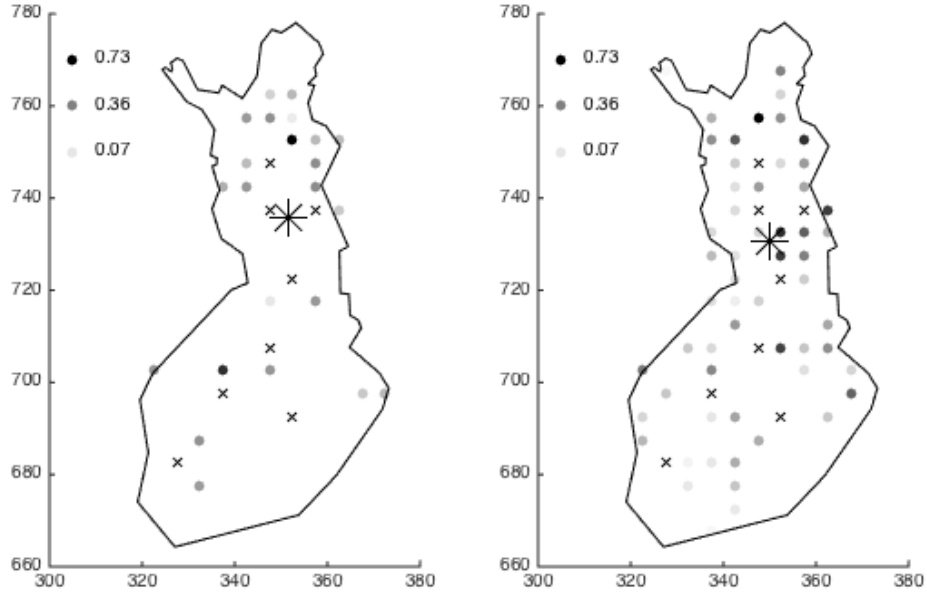
Supplementary fig. 46. Dryocopus martius



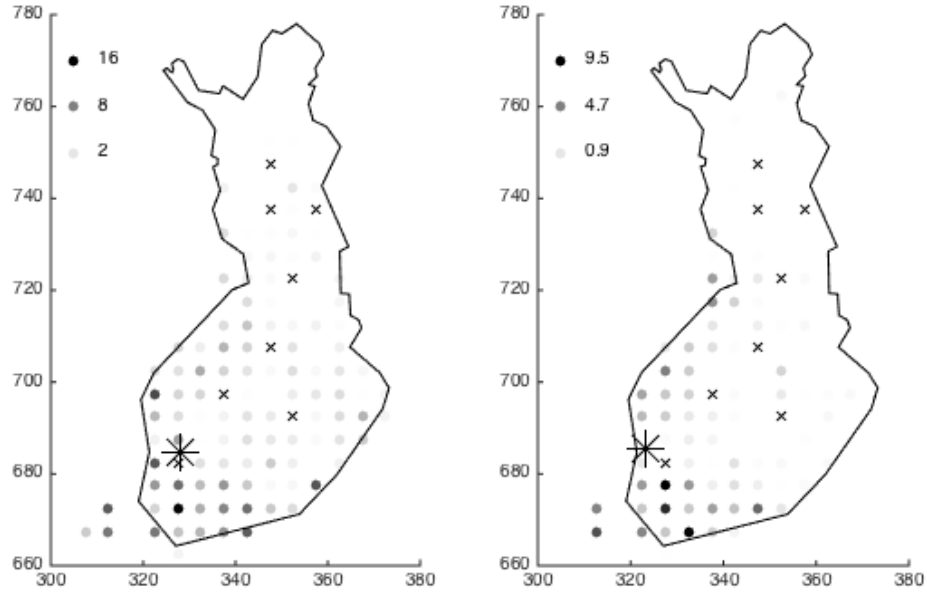
Supplementary fig. 47. Dendrocopos major



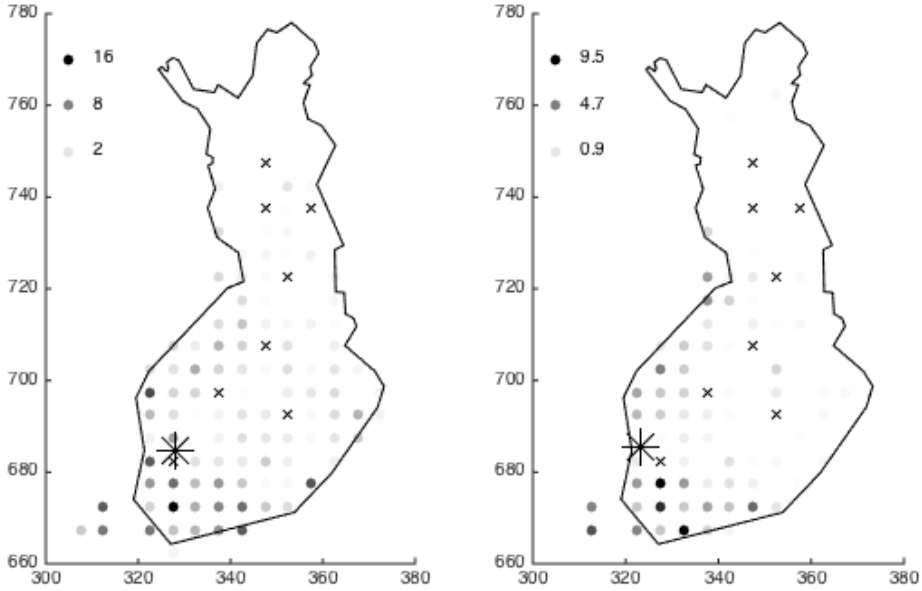
Supplementary fig. 48. Dendrocopos minor



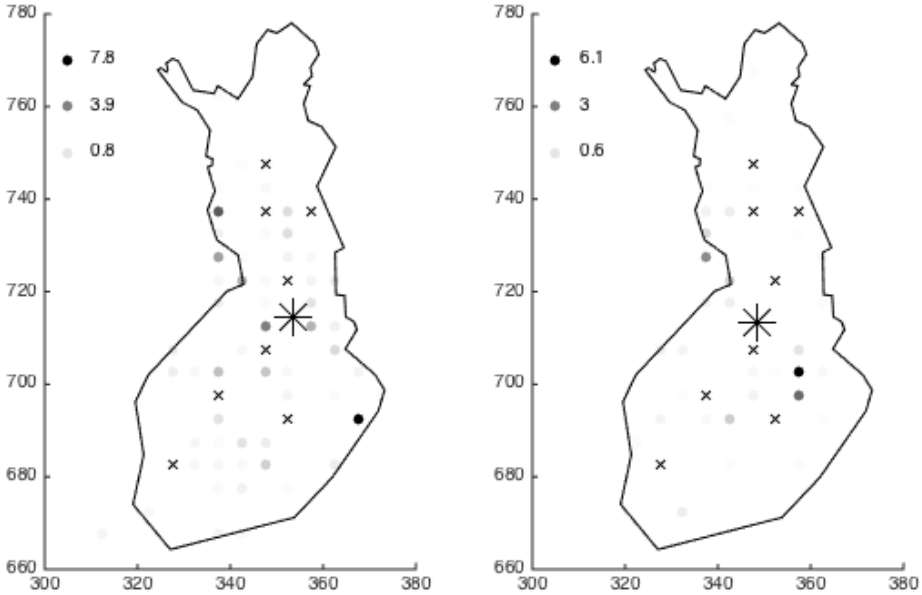
Supplementary fig. 49. Picoides tridactylus



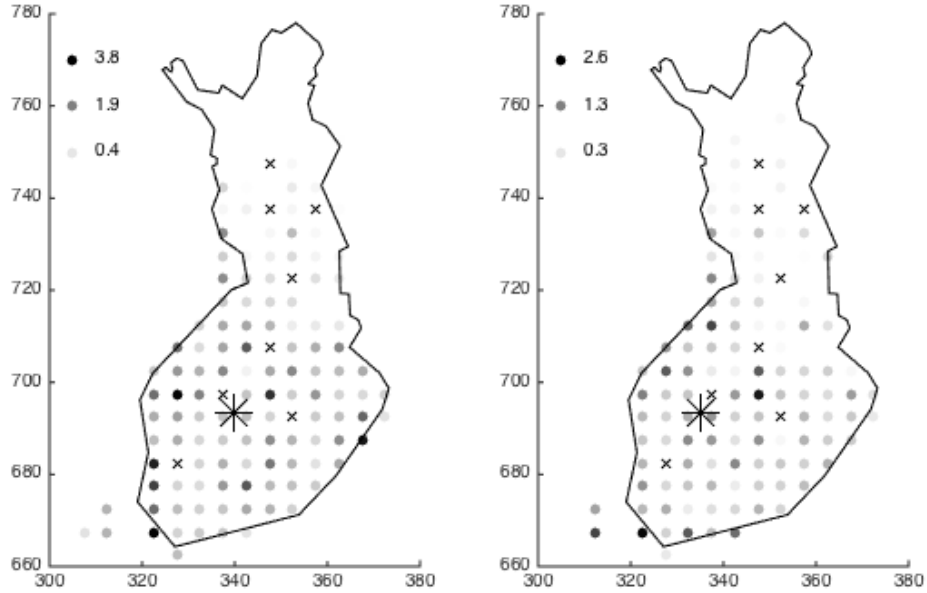
Supplementary fig. 50. Lullula arborea



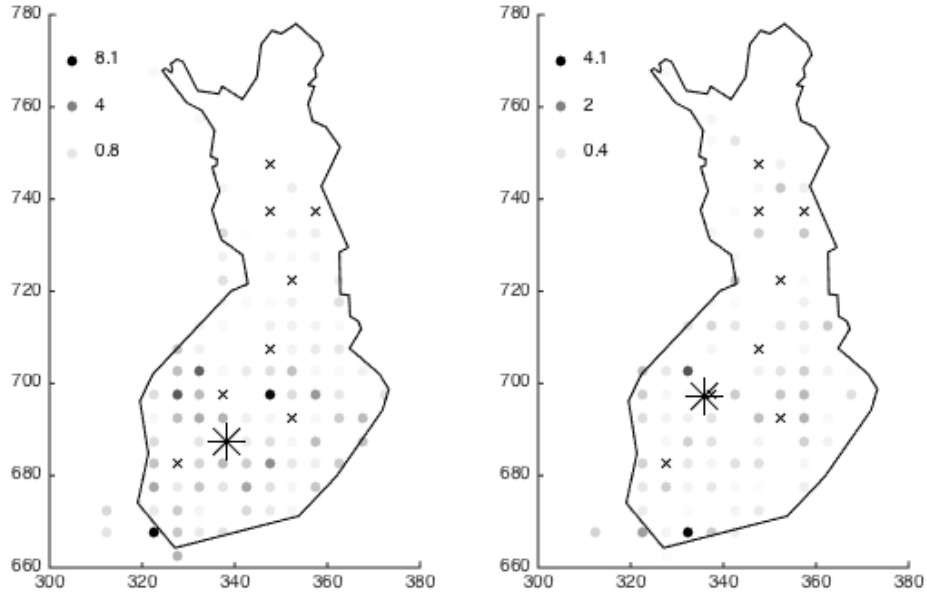
Supplementary fig. 51. Alauda arvensis



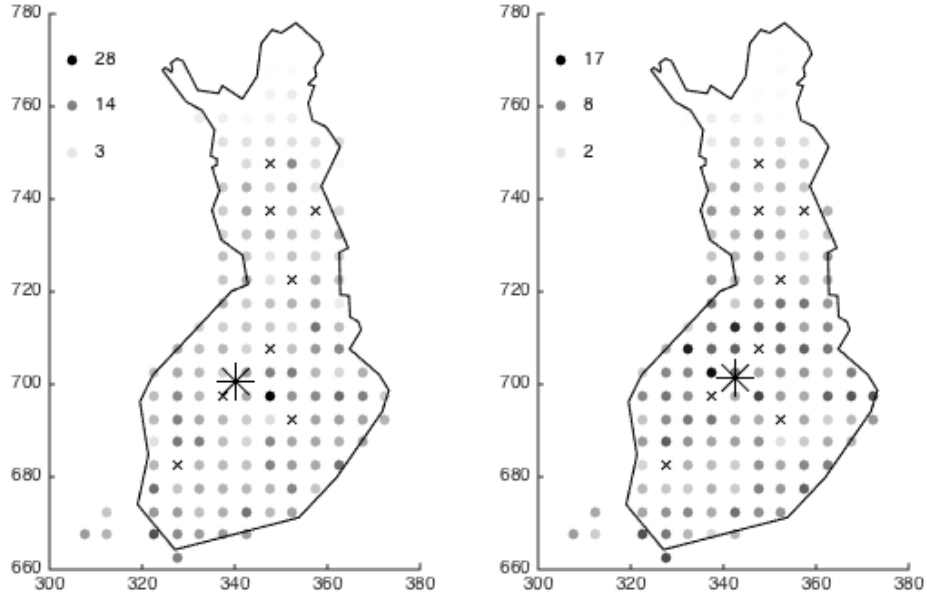
Supplementary fig. 52. Riparia riparia



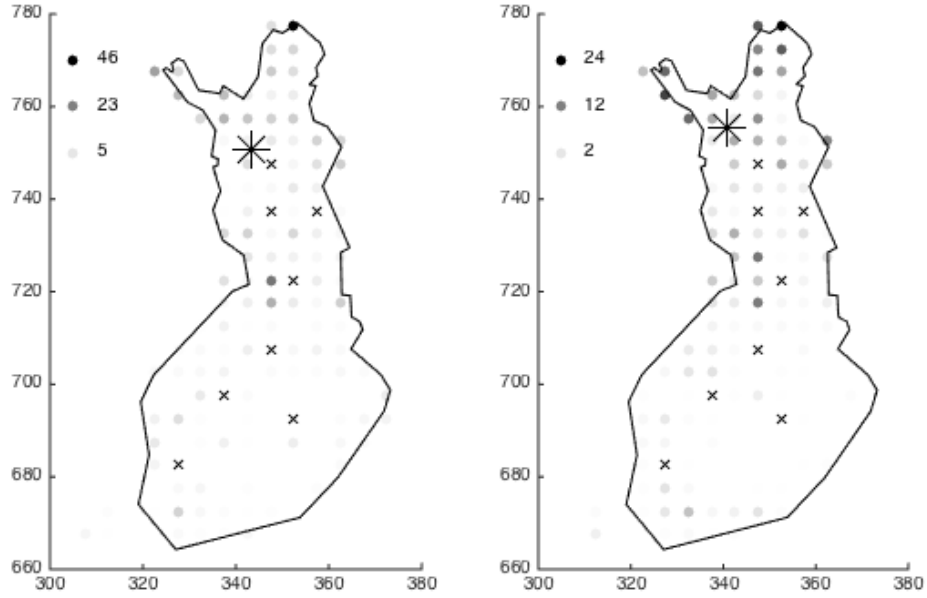
Supplementary fig. 53. Hirundo rustica



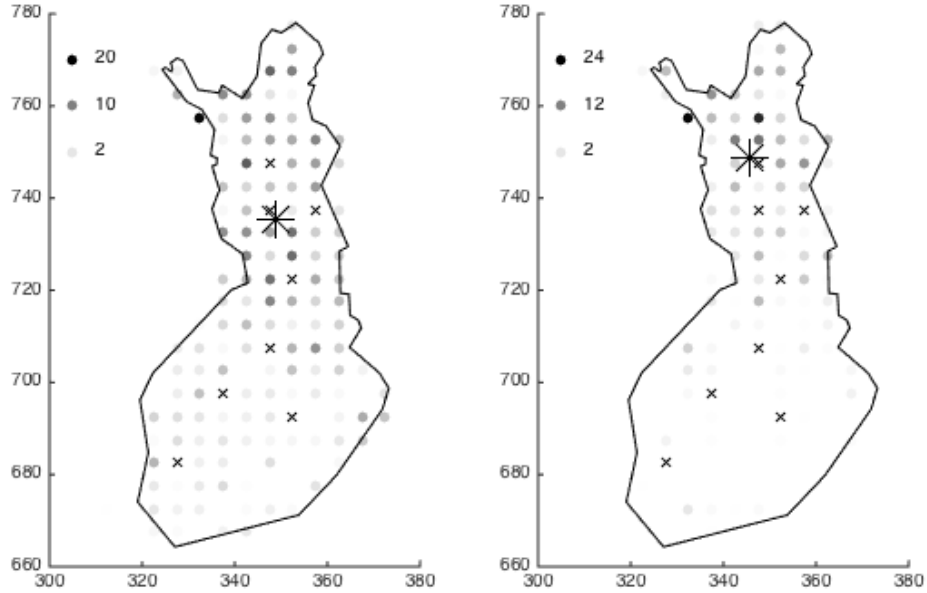
Supplementary fig. 54. Delichon urbicum



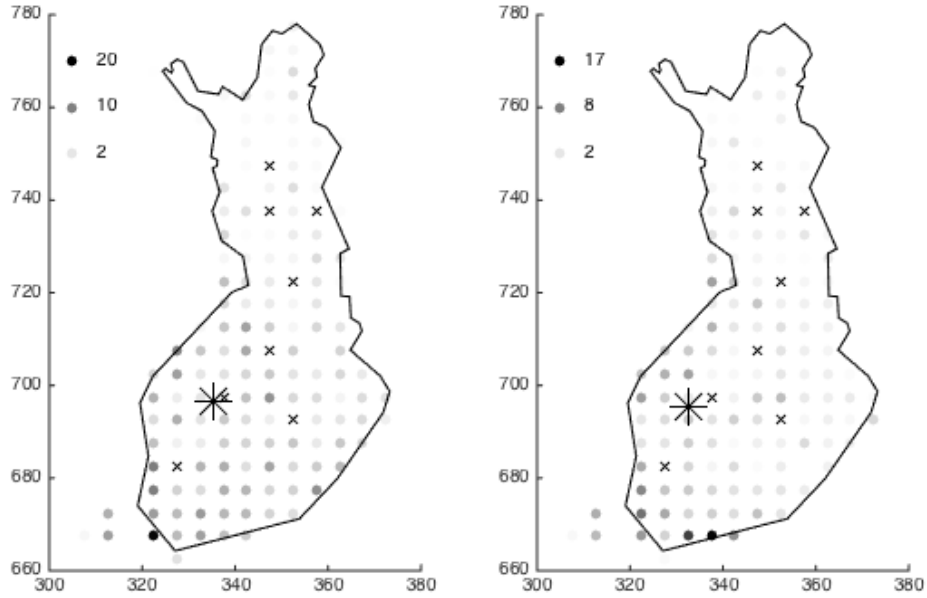
Supplementary fig. 55. Anthus trivialis



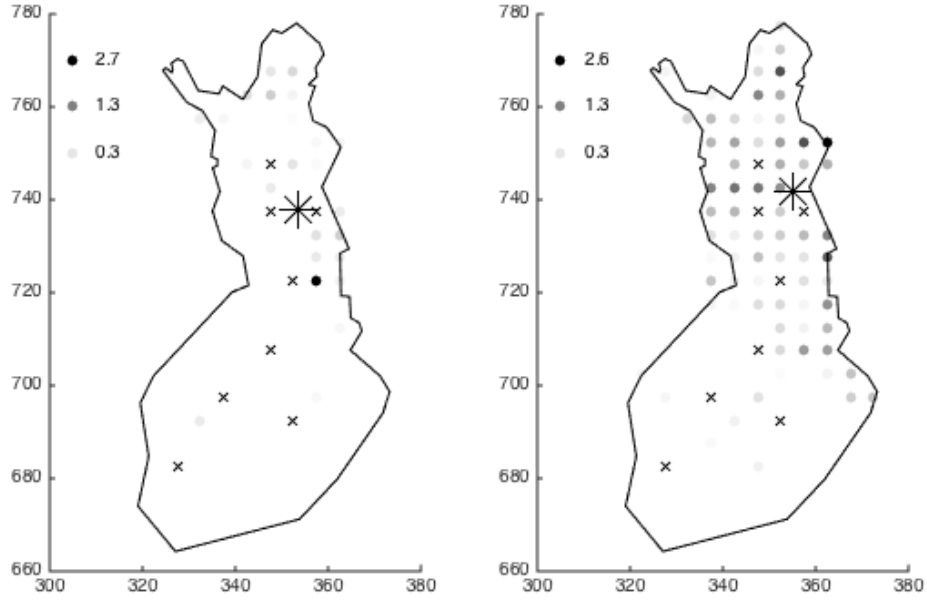
Supplementary fig. 56. Anthus prantensis



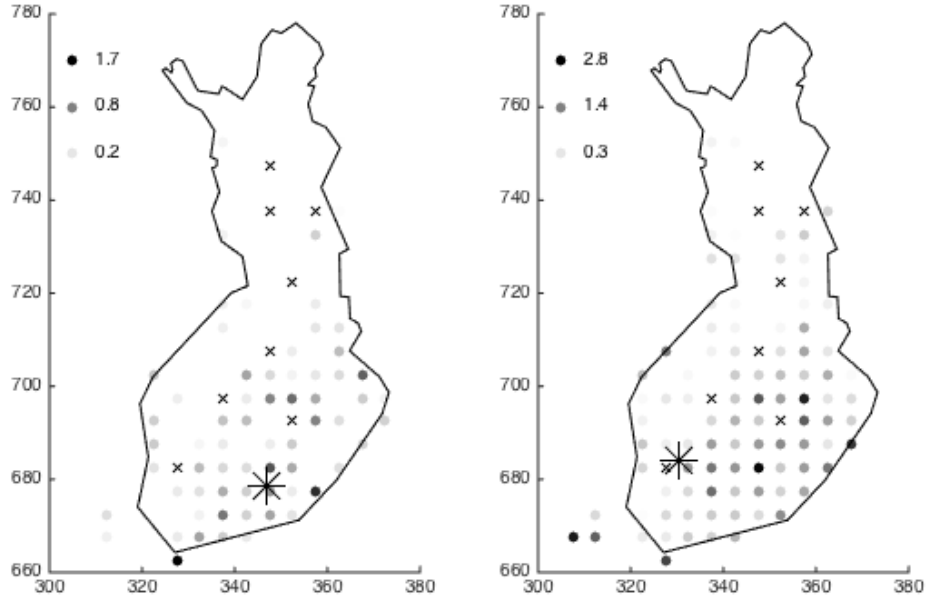
Supplementary fig. 57. Motacilla flava



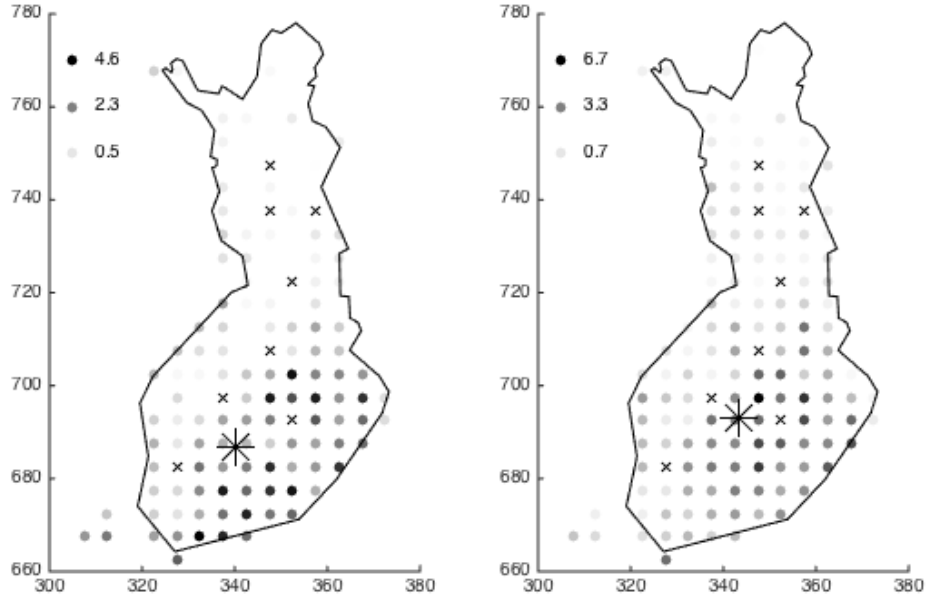
Supplementary fig. 58. Motacilla alba



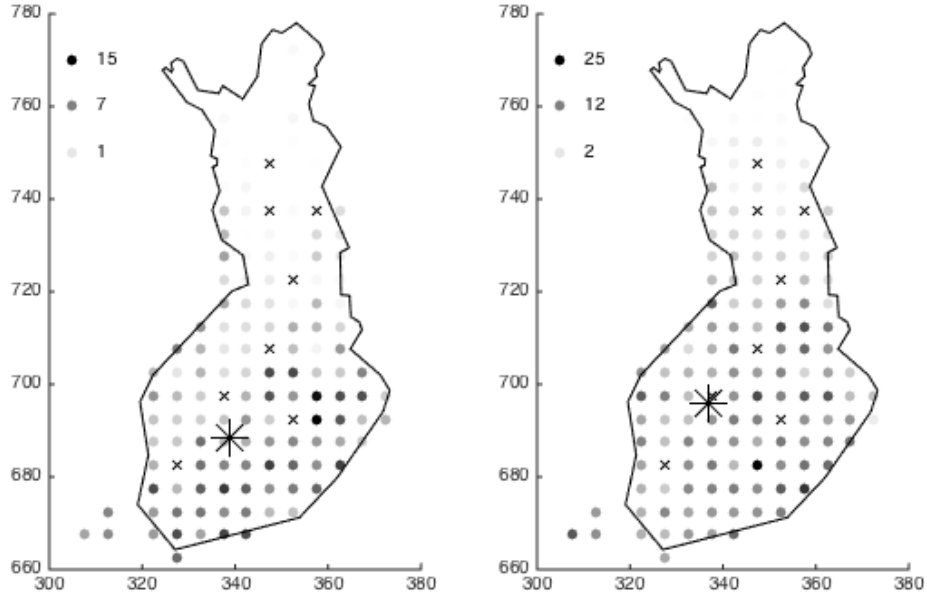
Supplementary fig. 59. Bombycilla garrulus



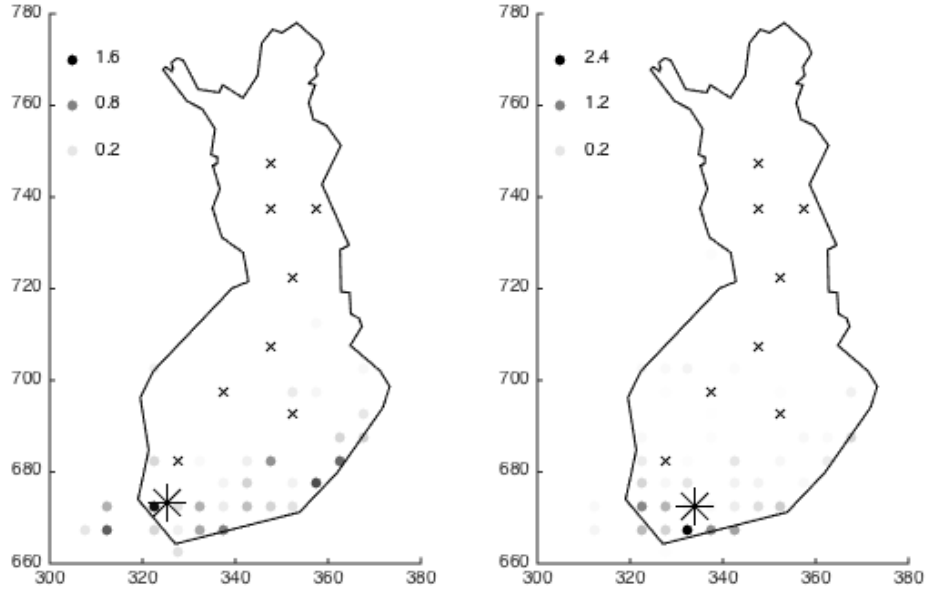
Supplementary fig. 60. Troglodytes troglodytes



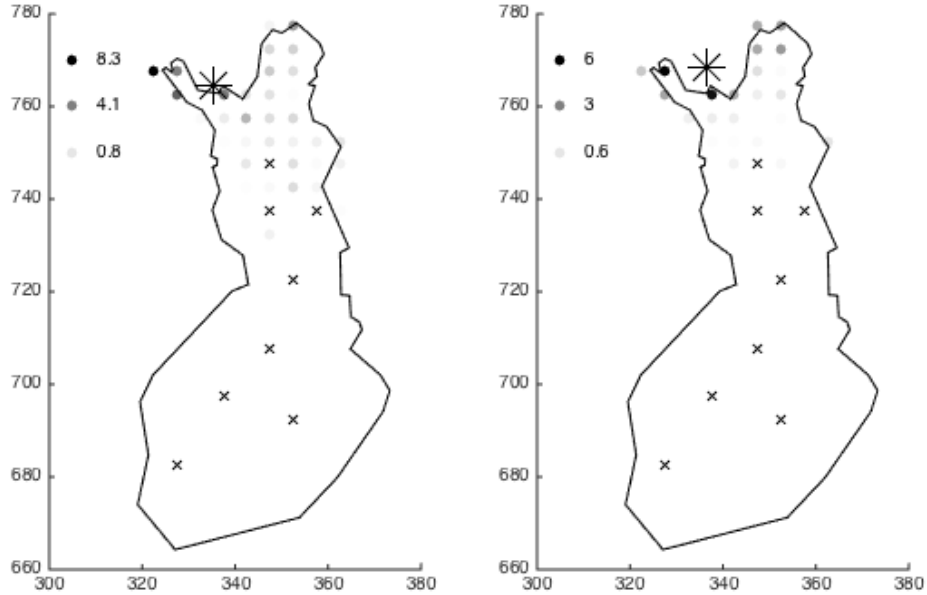
Supplementary fig. 61. Prunella modularis



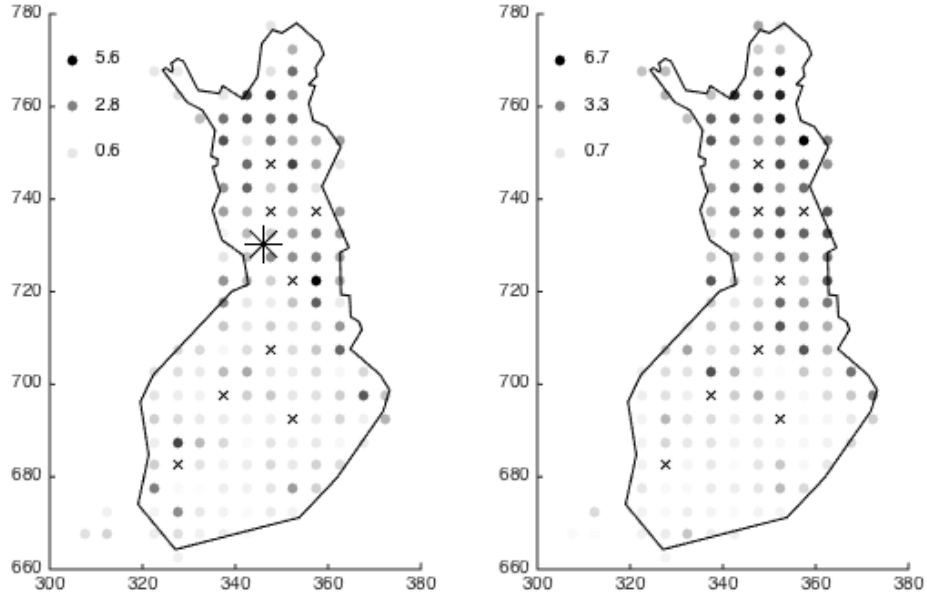
Supplementary fig. 62. Erithacus rubecula



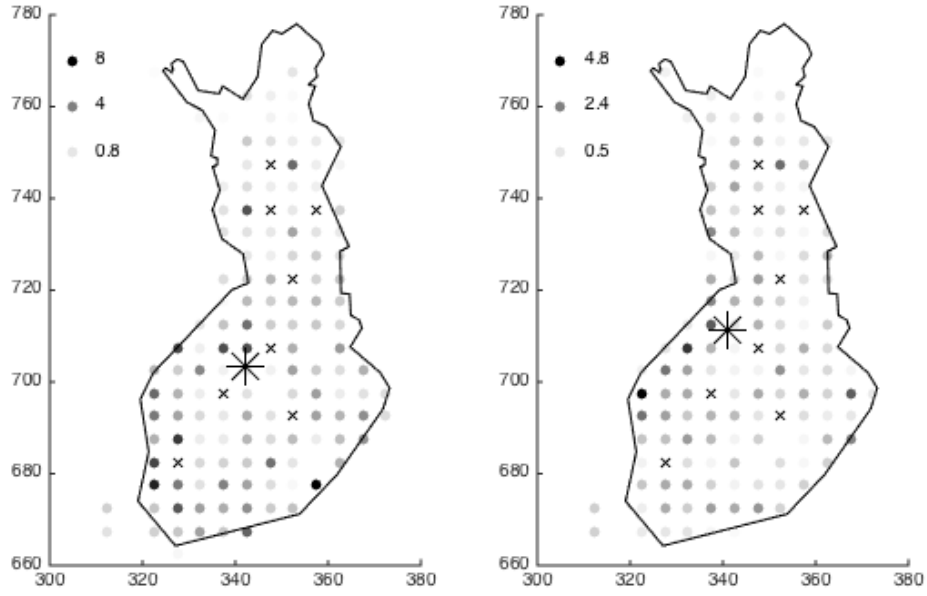
Supplementary fig. 63. Luscinia luscinia



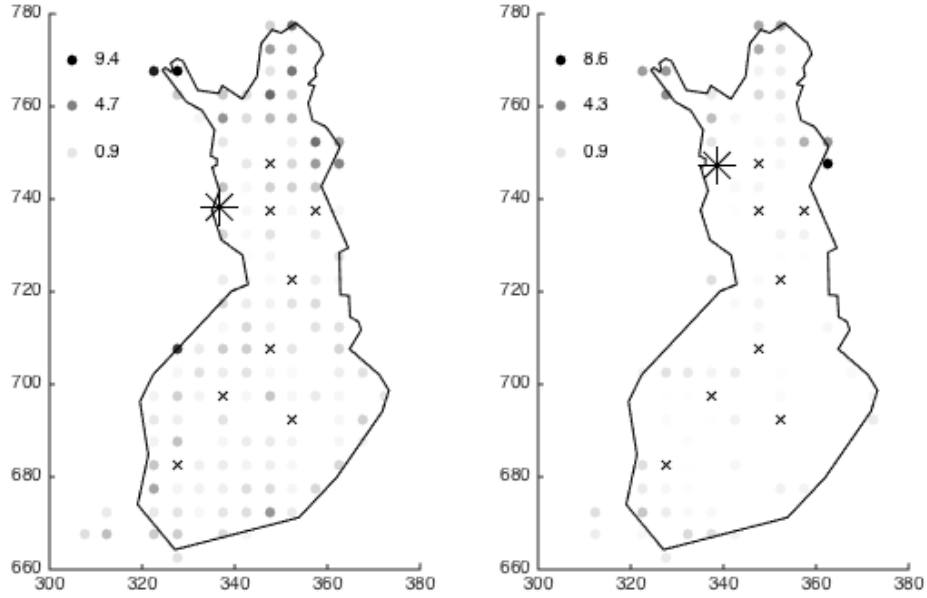
Supplementary fig. 64. Luscinia svecica



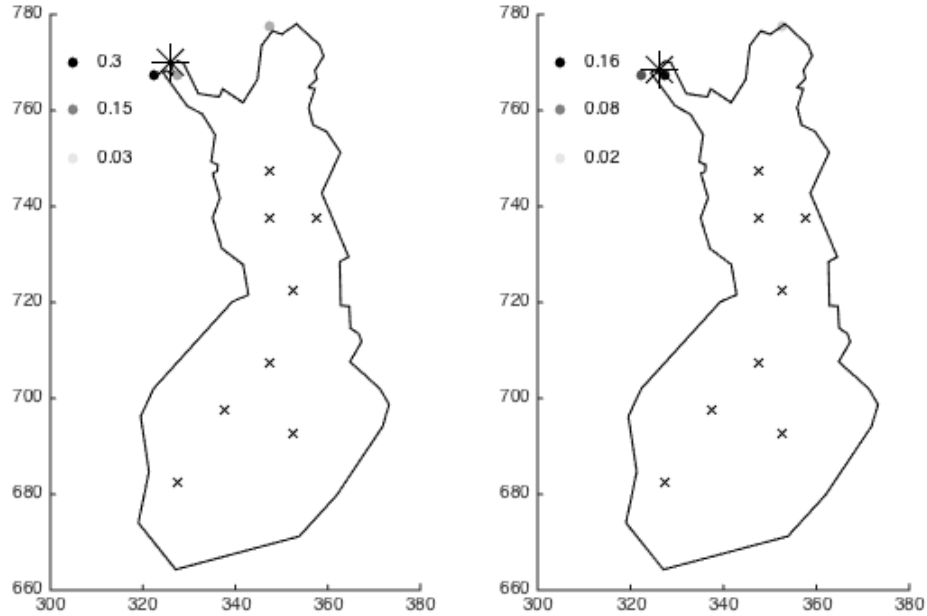
Supplementary fig. 65. Phoenicurus phoenicurus



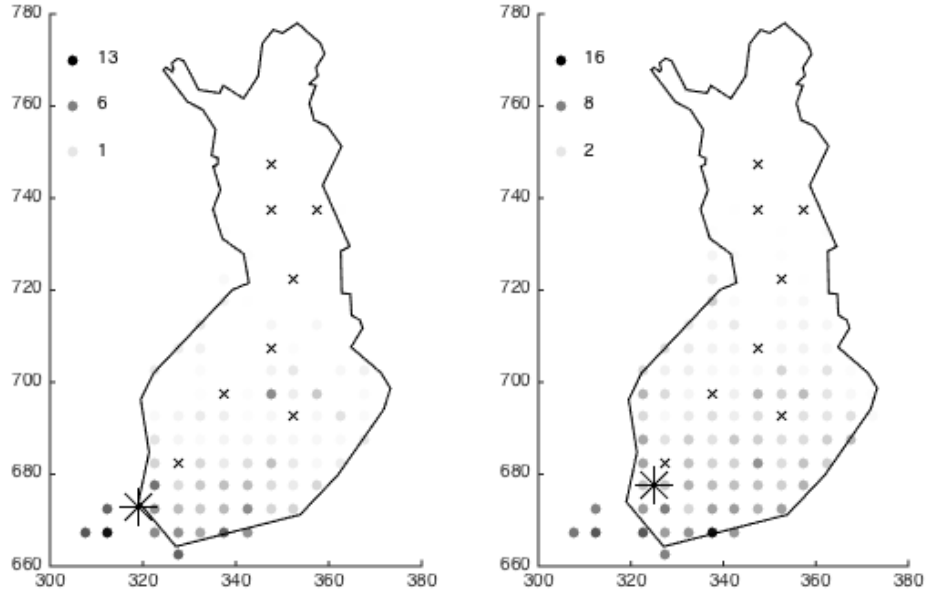
Supplementary fig. 66. Saxicola rubetra



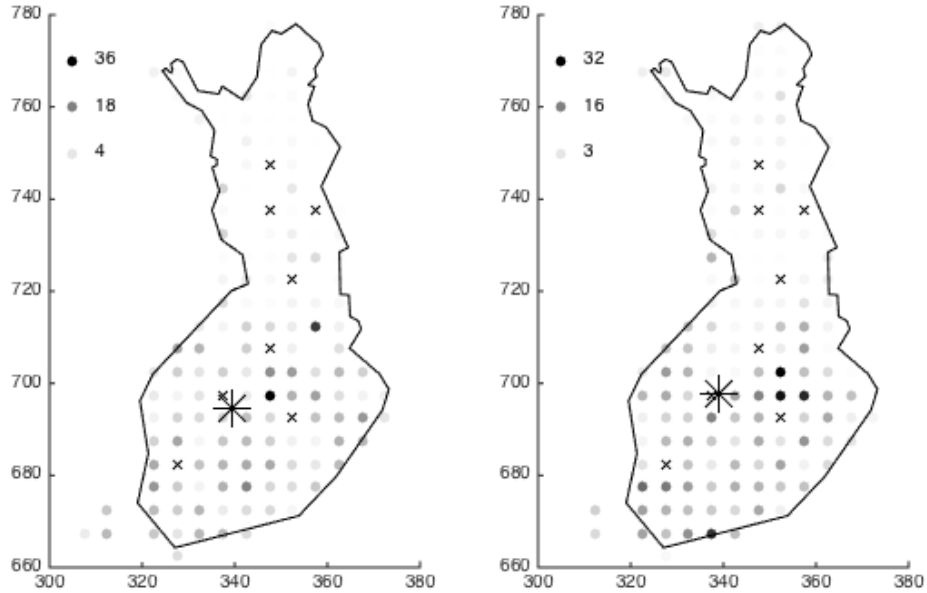
Supplementary fig. 67. Oenanthe oenanthe



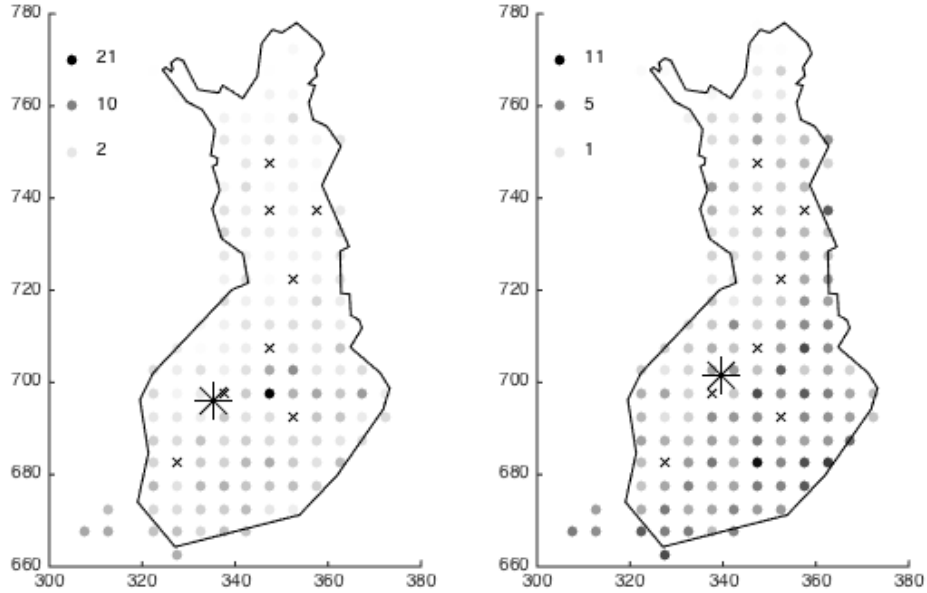
Supplementary fig. 68. Turdus torquatus



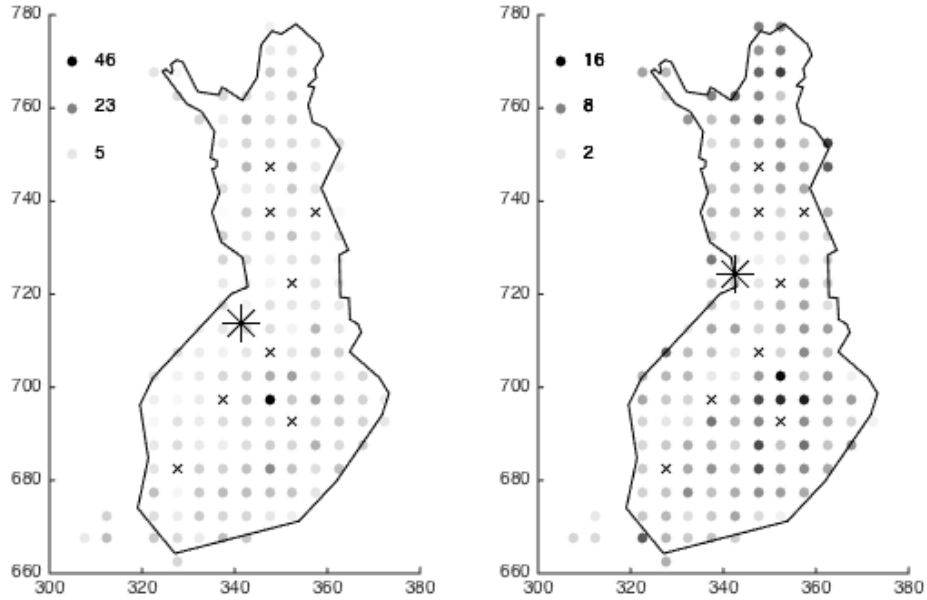
Supplementary fig. 69. Turdus merula



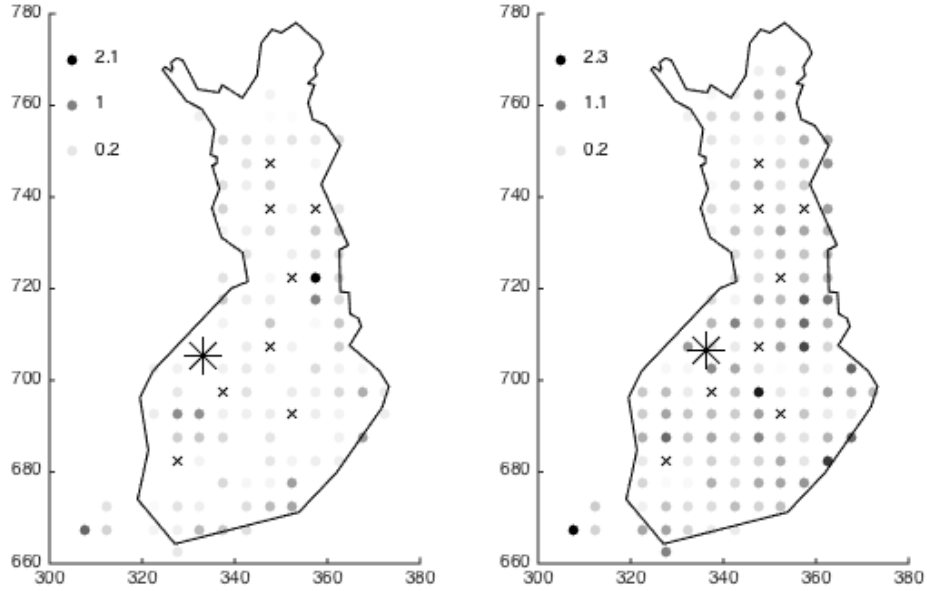
Supplementary fig. 70. Turdus pilaris



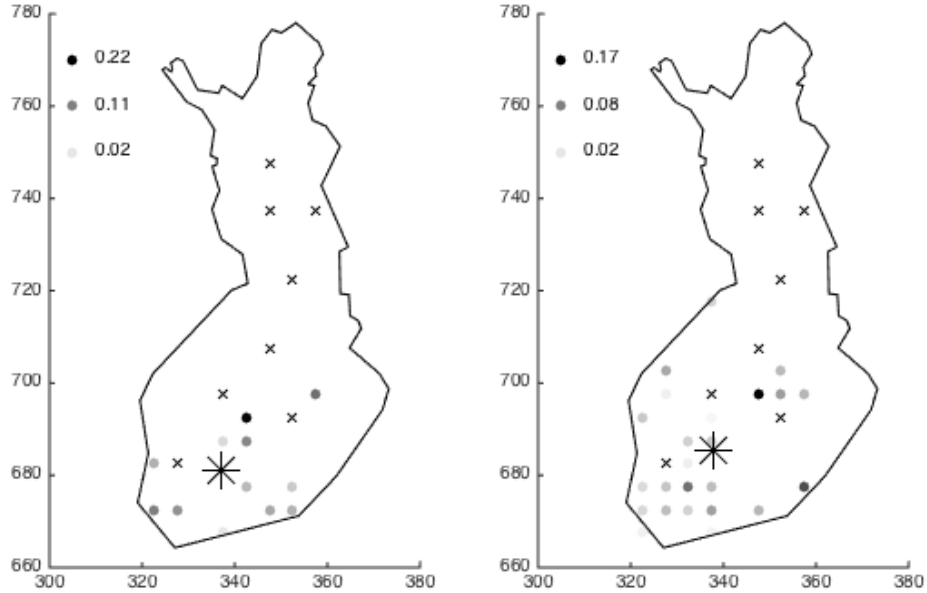
Supplementary fig. 71. Turdus philomelos



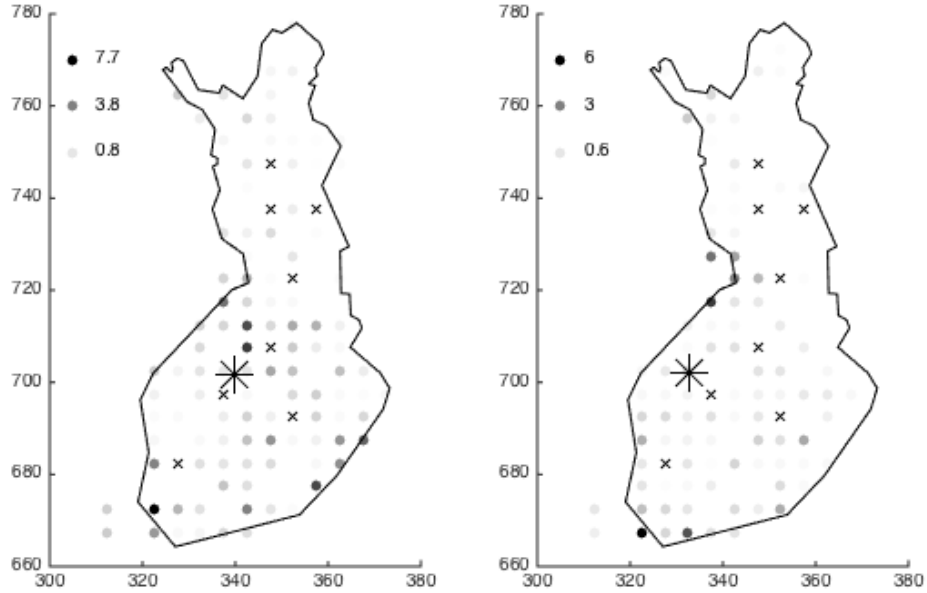
Supplementary fig. 72. Turdus iliacus



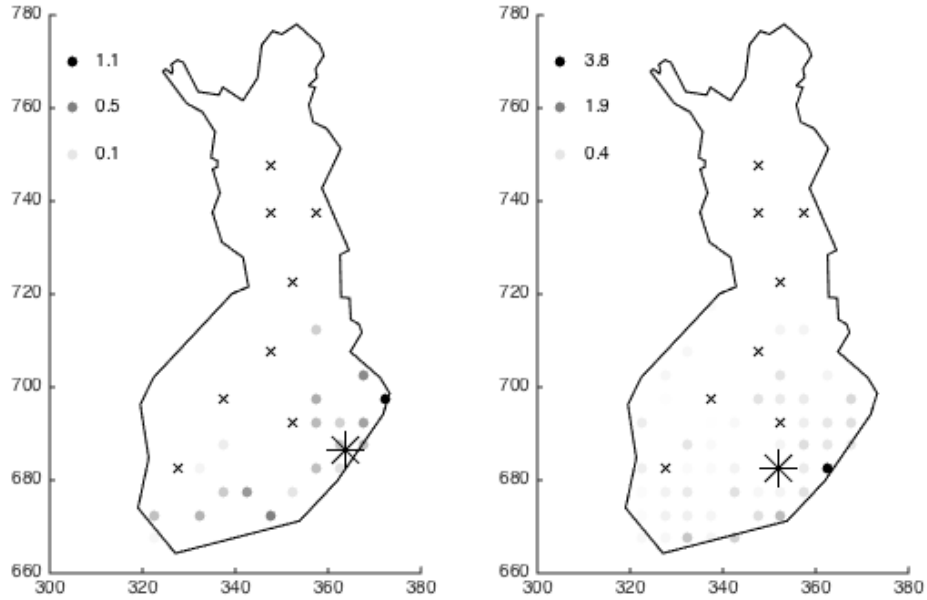
Supplementary fig. 73. Turdus viscivorus



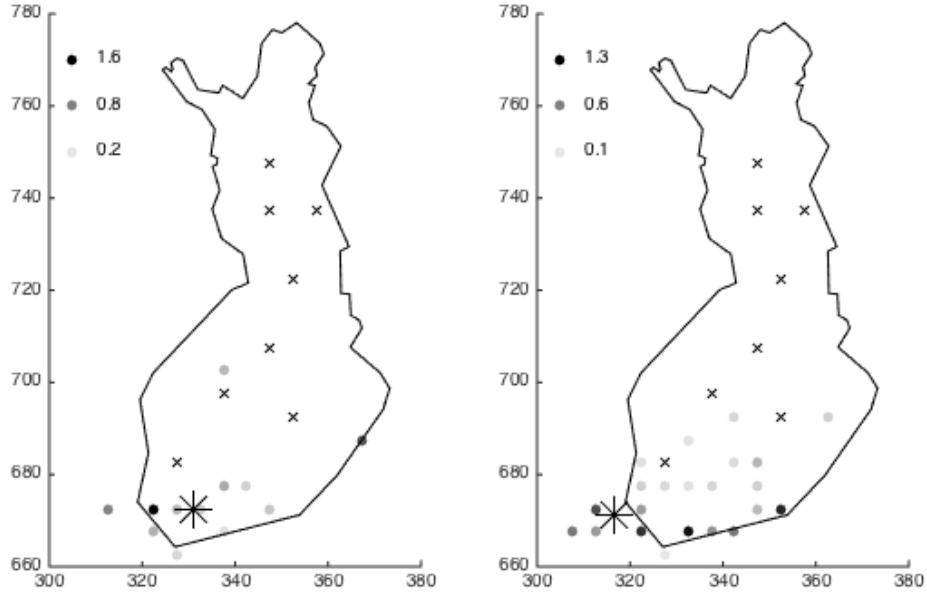
Supplementary fig. 74. Locustella naevia



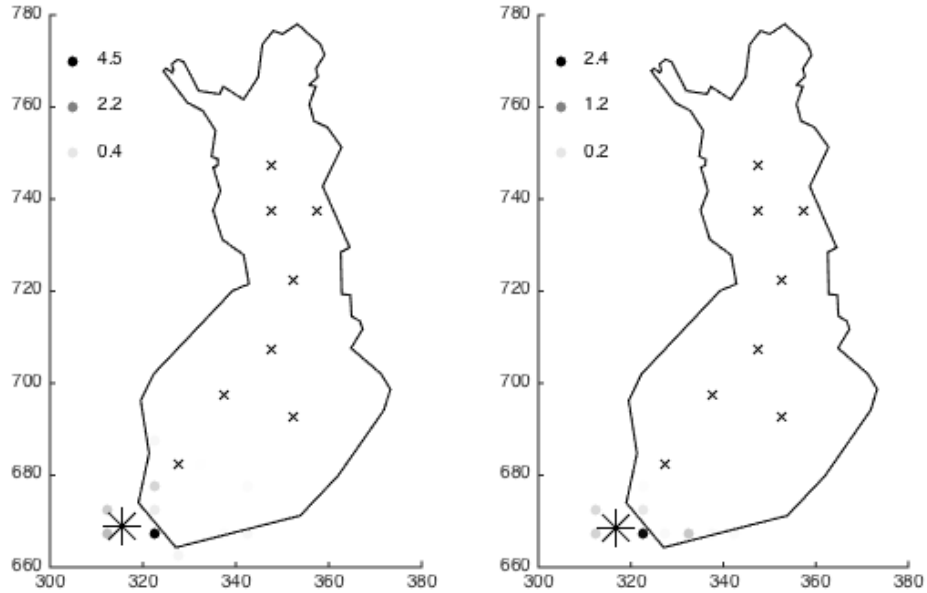
Supplementary fig. 75. Acrocephalus schoenobaenus



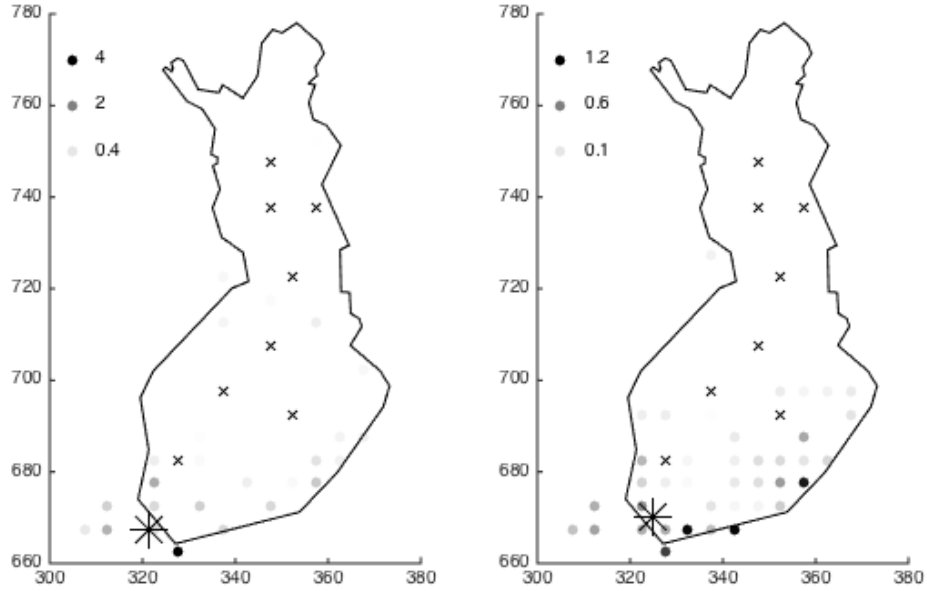
Supplementary fig. 76. Acrocephalus dumetorum



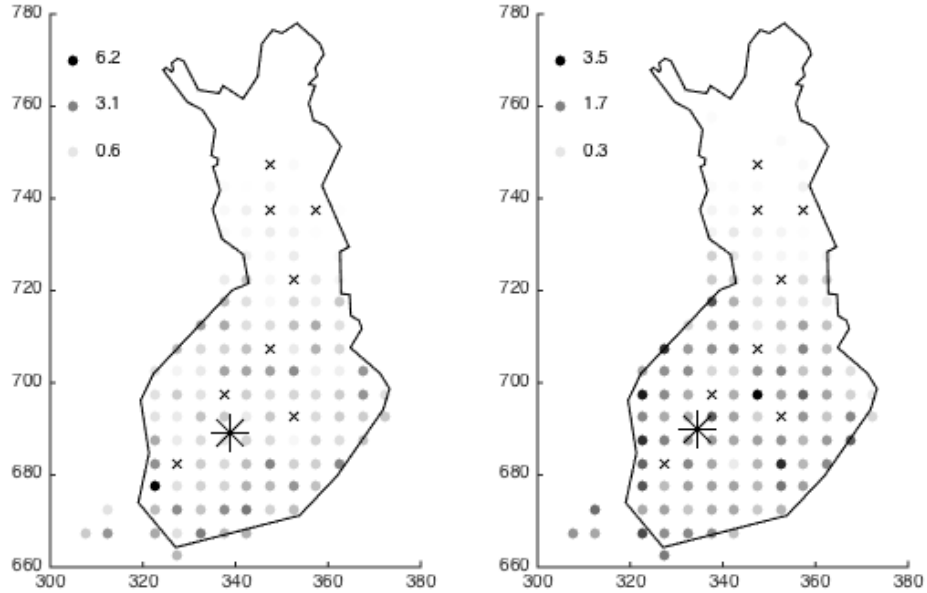
Supplementary fig. 77. Acrocephalus palustris



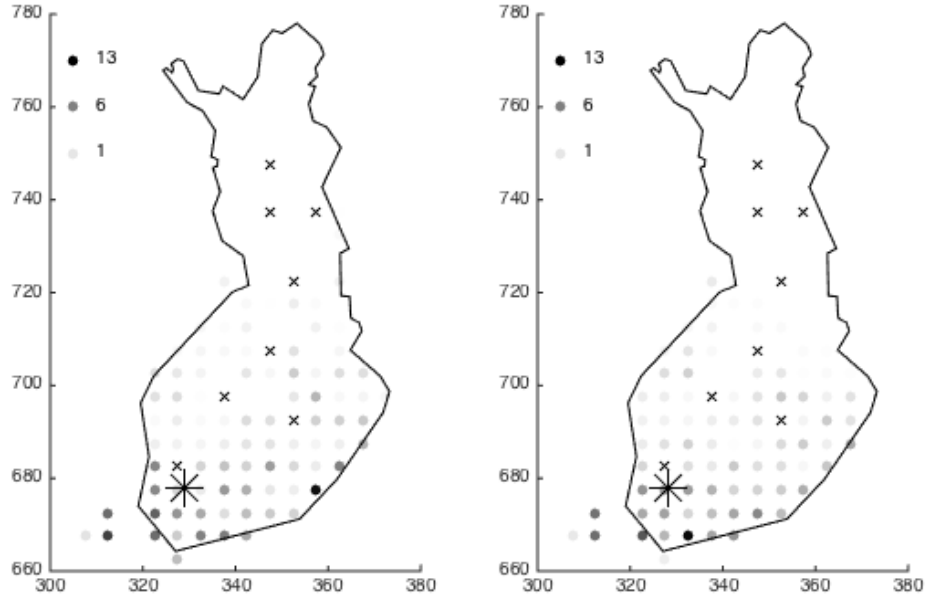
Supplementary fig. 78. Acrocephalus scirpaceus



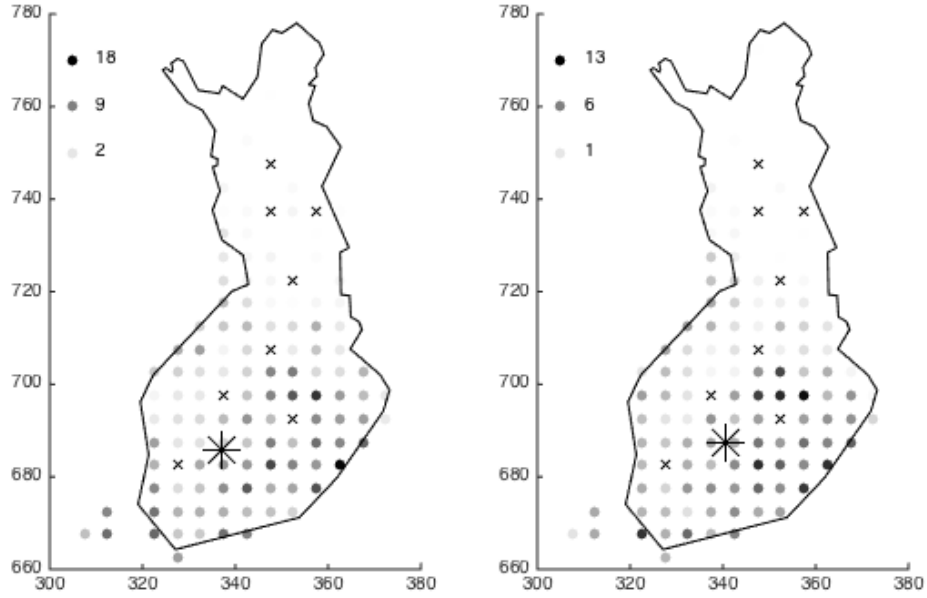
Supplementary fig. 79. Hippolais icterina



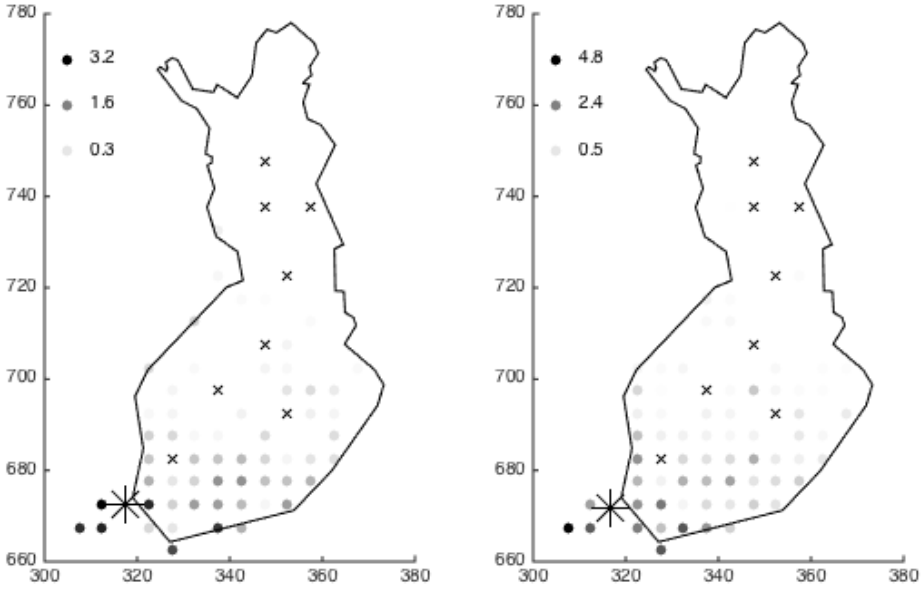
Supplementary fig. 80. Sylvia curruca



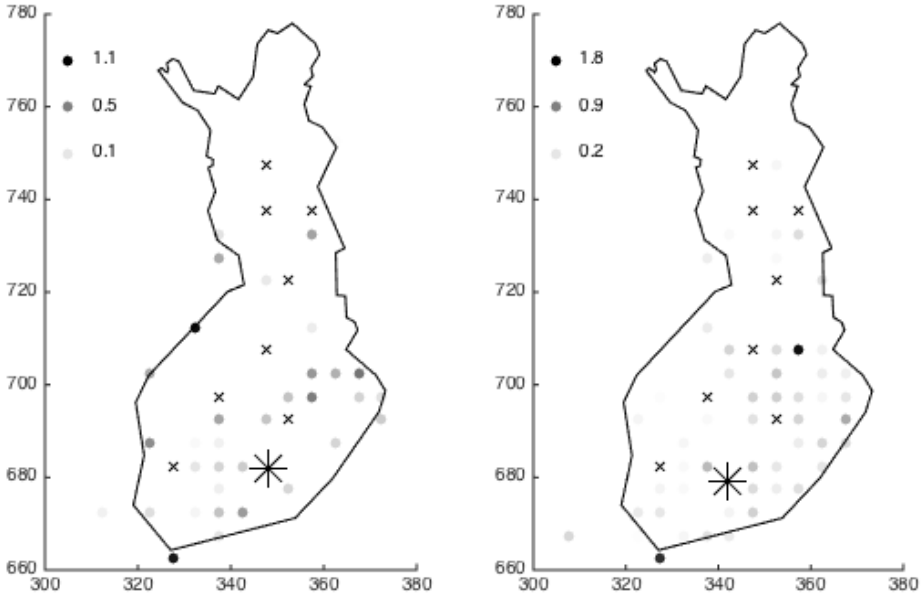
Supplementary fig. 81. Sylvia communis



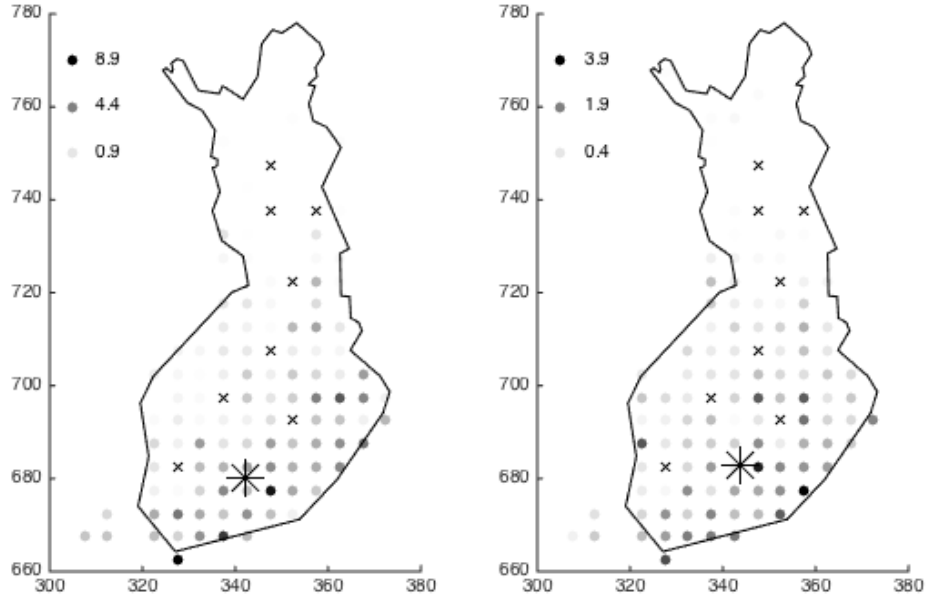
Supplementary fig. 82. Sylvia borin



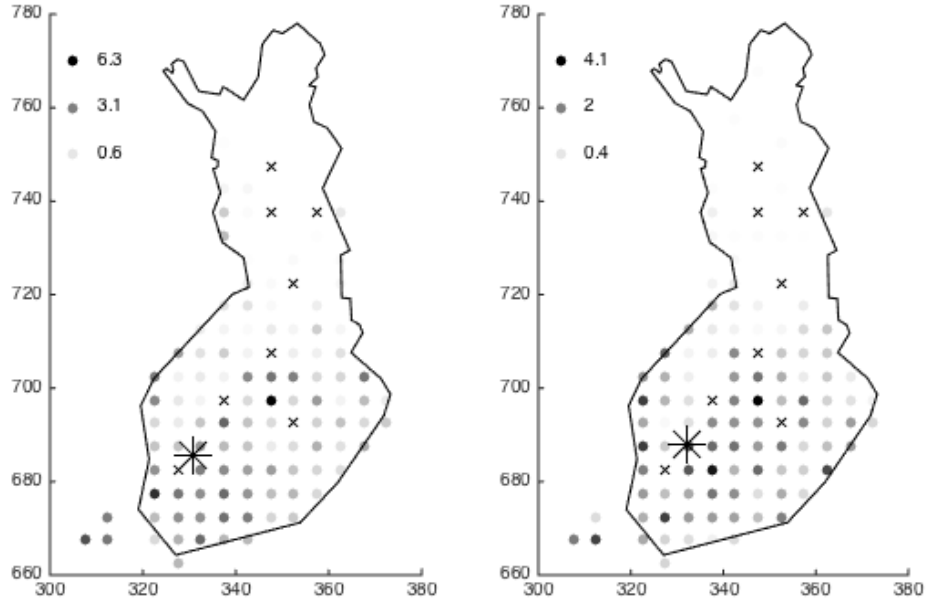
Supplementary fig. 83. Sylvia atricapilla



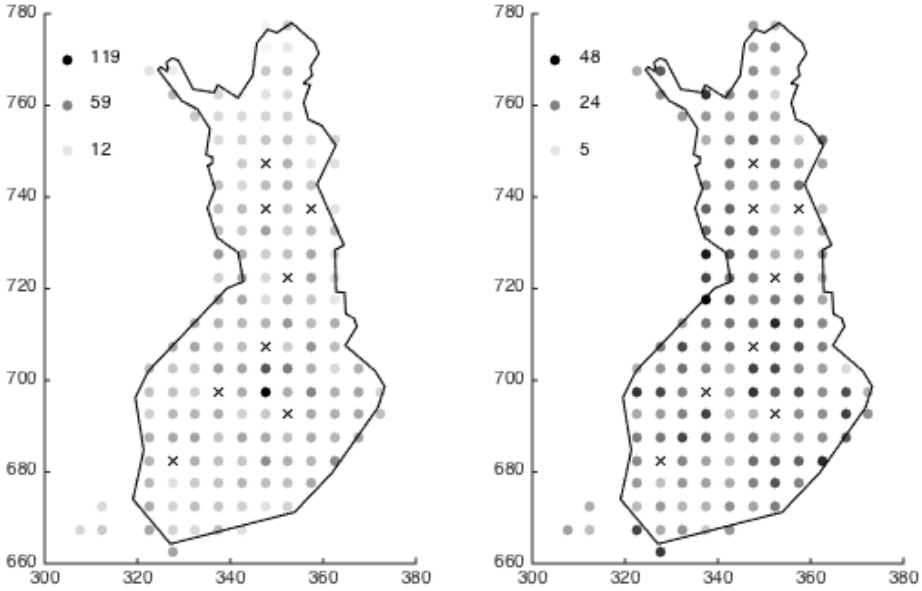
Supplementary fig. 84. Phylloscopus trochiloides



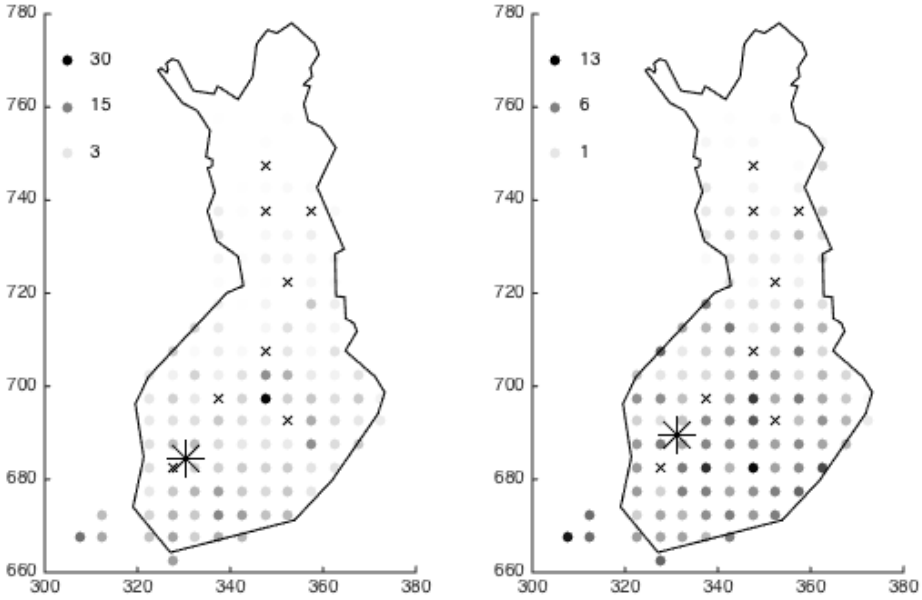
Supplementary fig. 85. Phylloscopus sibilatrix



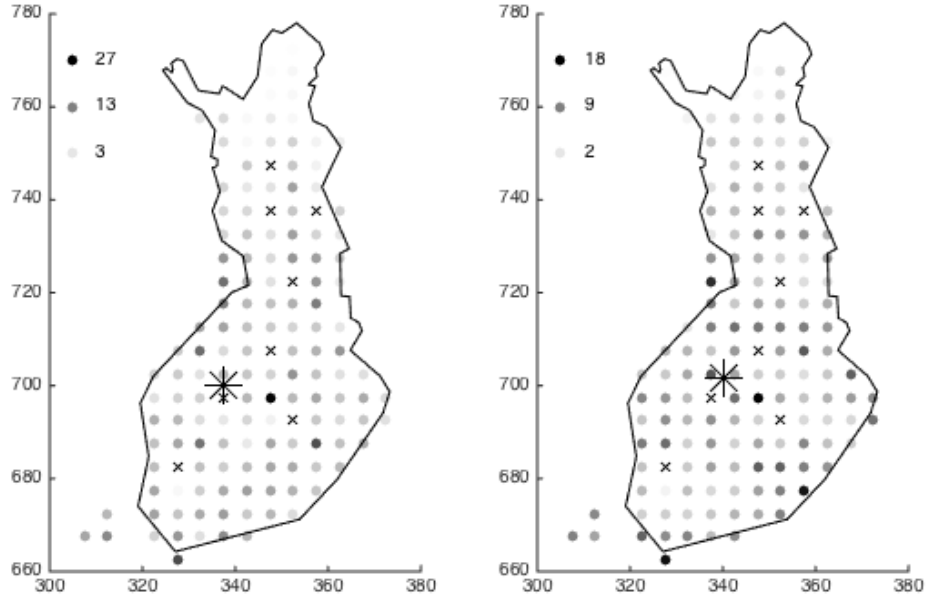
Supplementary fig. 86. Phylloscopus collybita



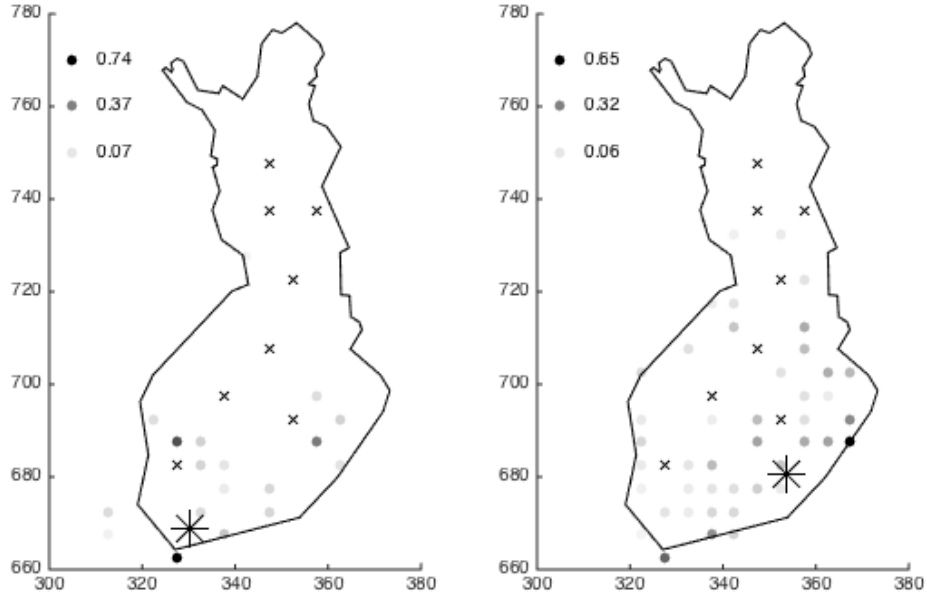
Supplementary fig. 87. Phylloscopus trochilus



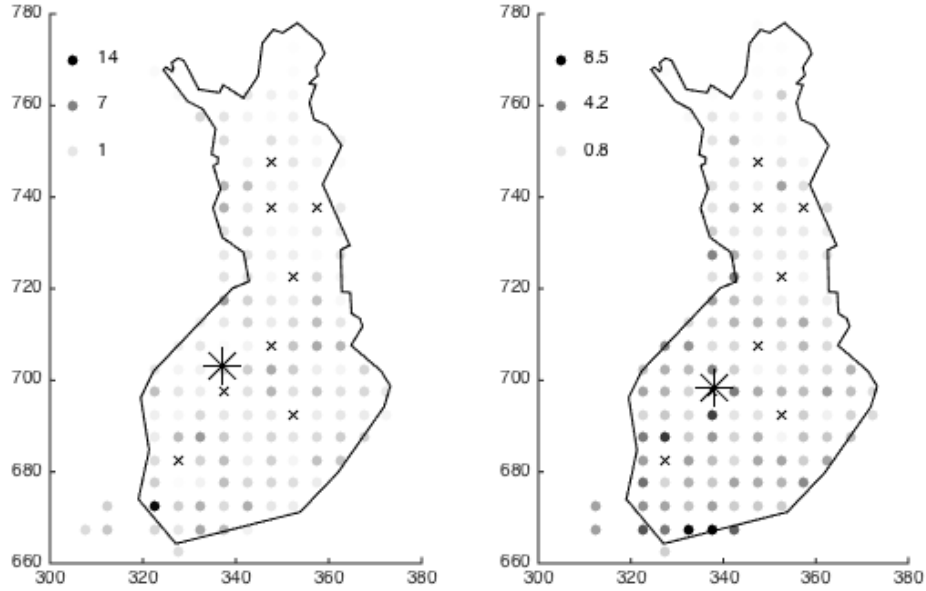
Supplementary fig. 88. Regulus regulus



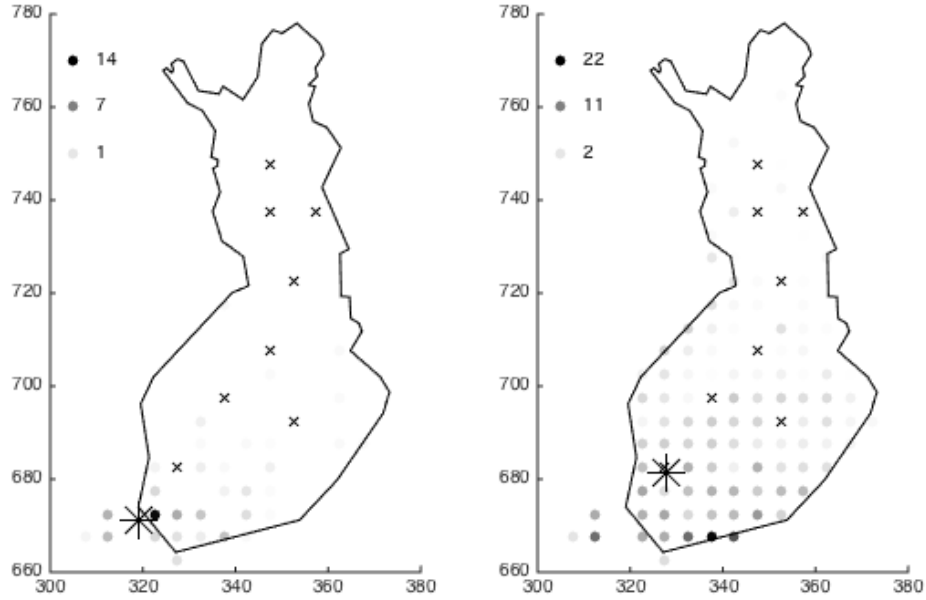
Supplementary fig. 89. Muscicapa striata



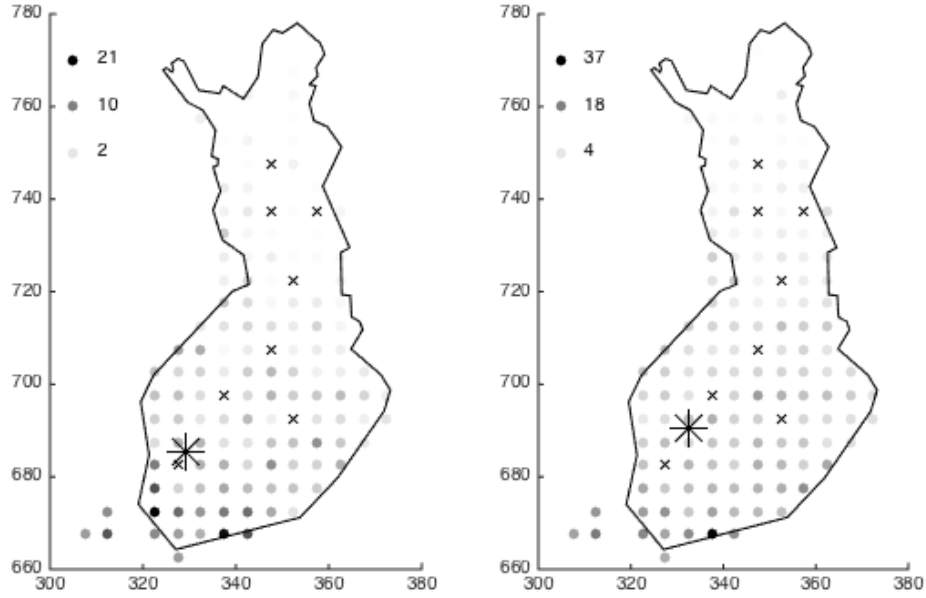
Supplementary fig. 90. Ficedula parva



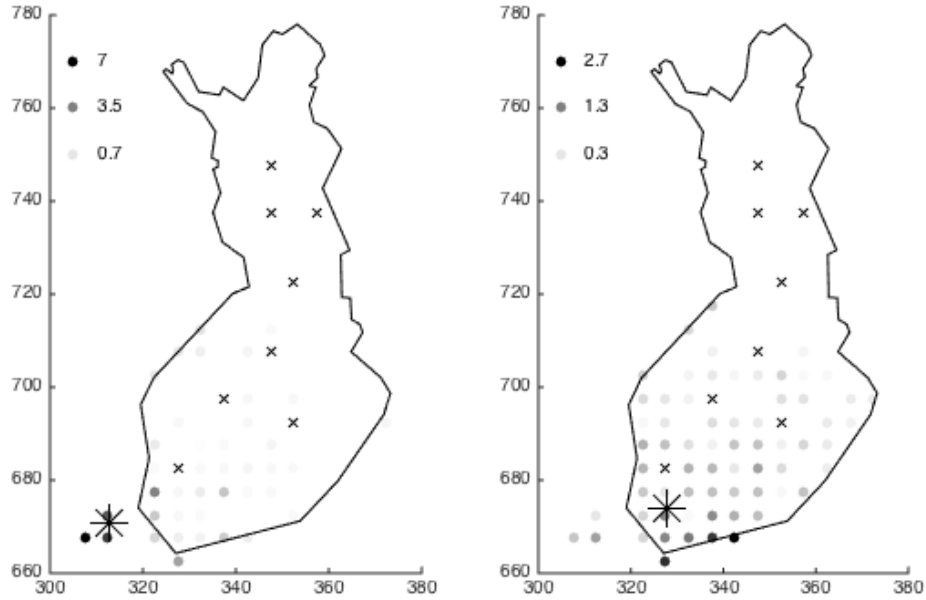
Supplementary fig. 91. Ficedula hypoleuca



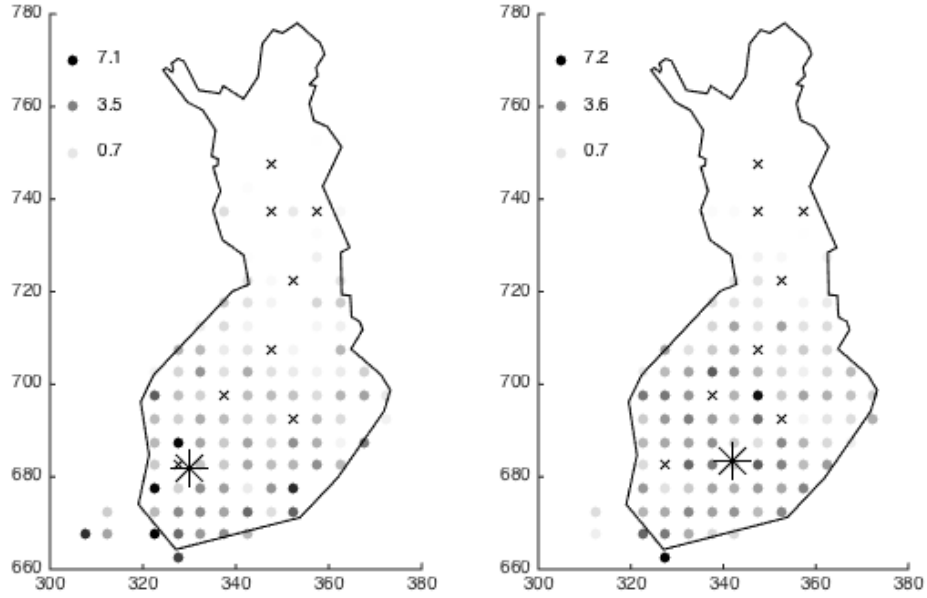
Supplementary fig. 92. Cyanistes caeruleus



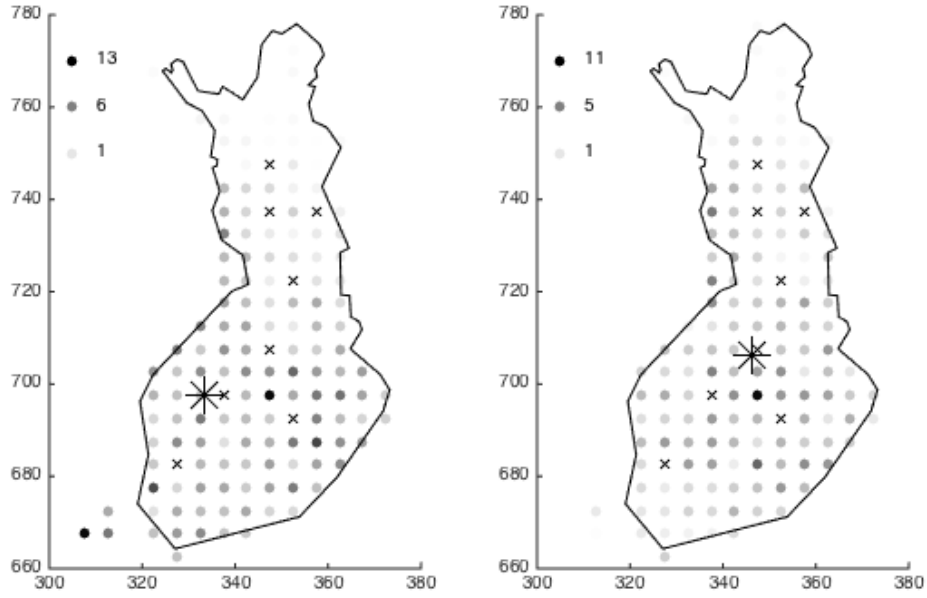
Supplementary fig. 93. Parus major



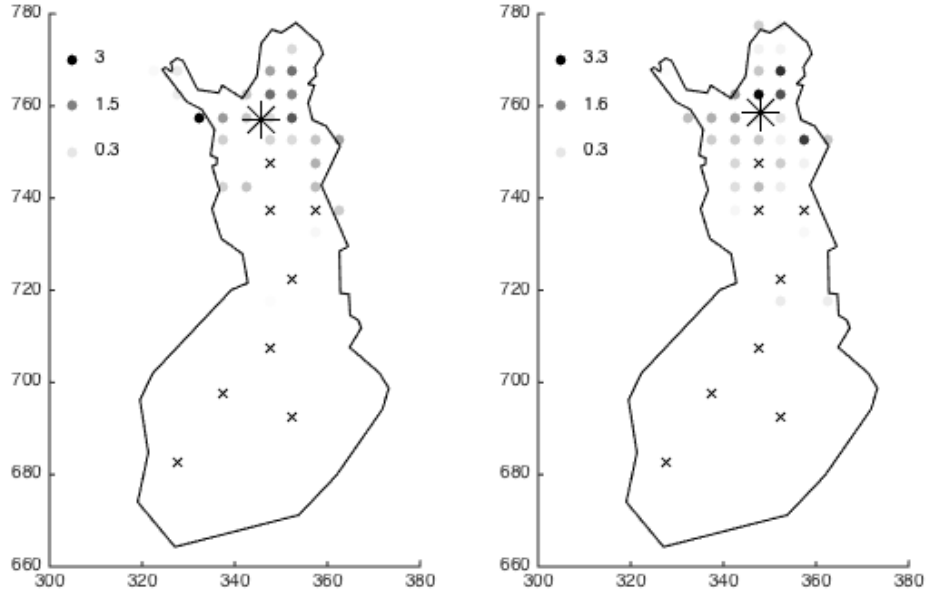
Supplementary fig. 94. Periparus ater



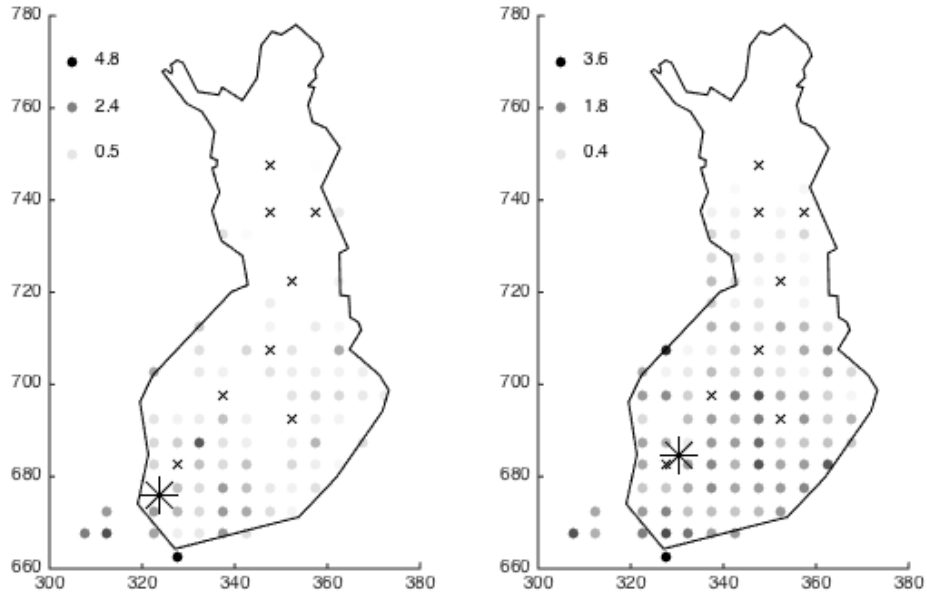
Supplementary fig. 95. Lophophanes cristatus



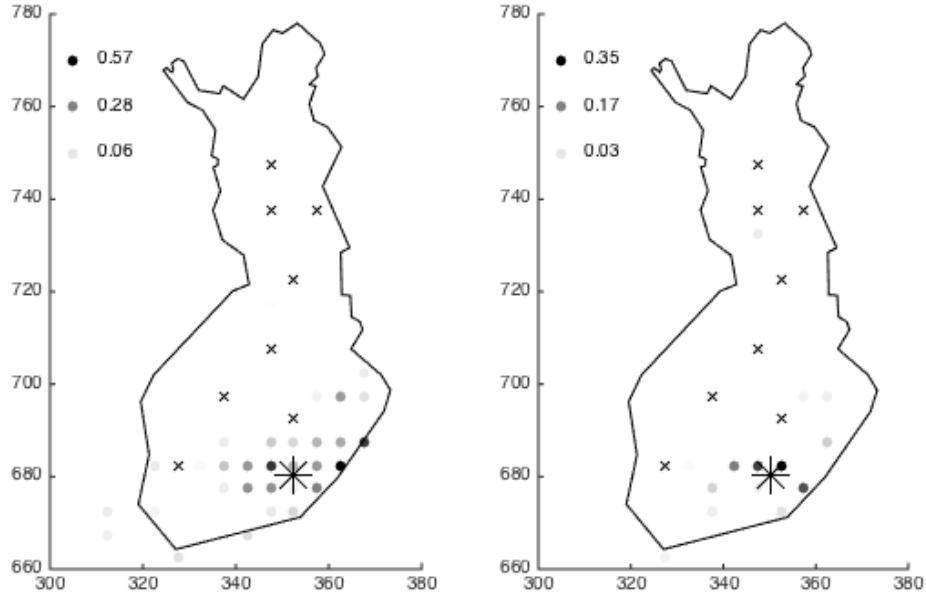
Supplementary fig. 96. Poecile montanus



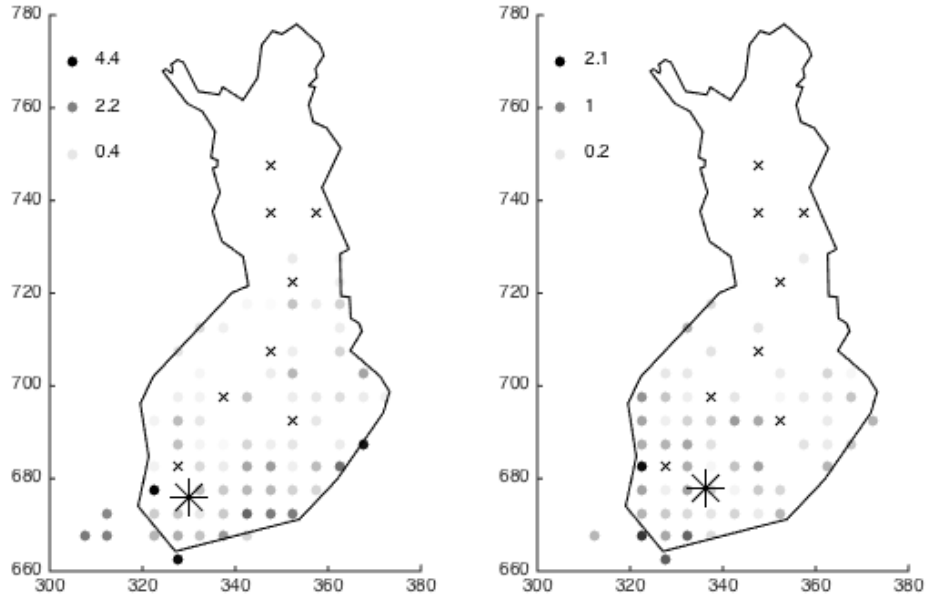
Supplementary fig. 97. Poecile cinctus



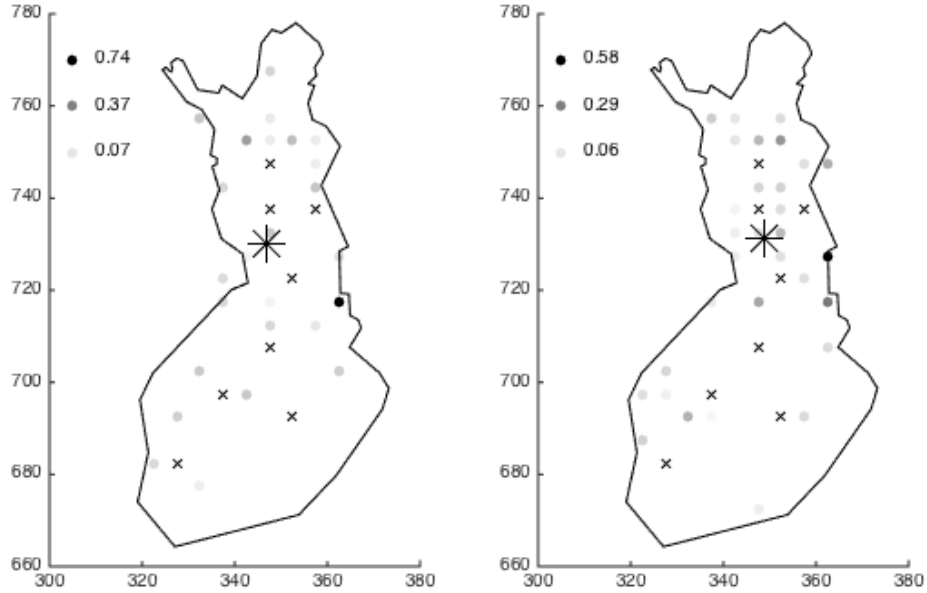
Supplementary fig. 98. Certhia familiaris



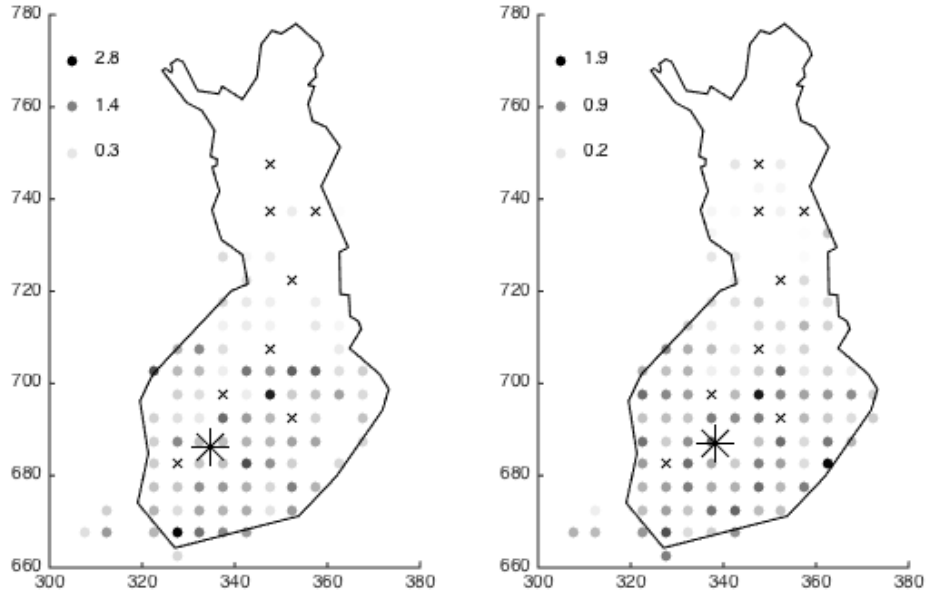
Supplementary fig. 99. Oriolus oriolus



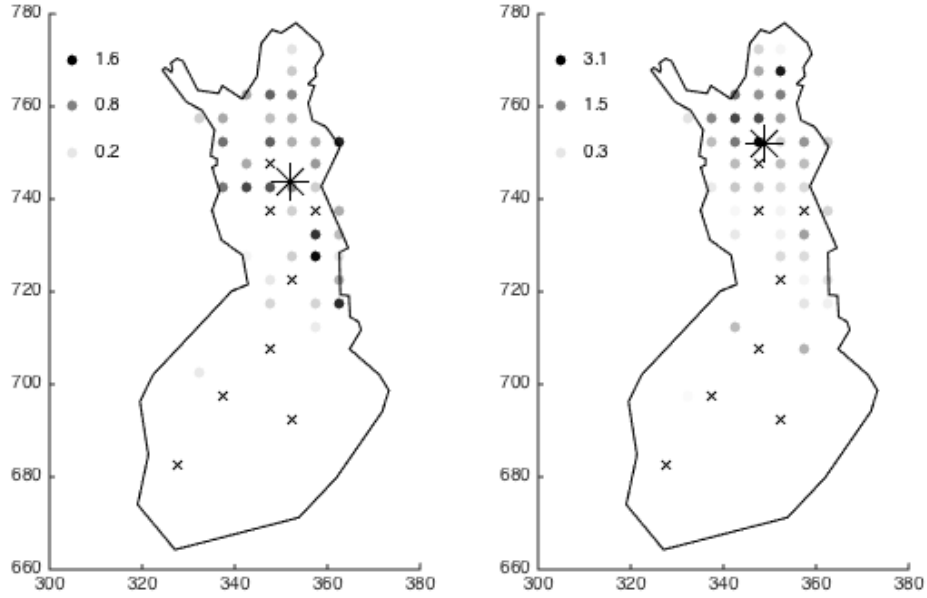
Supplementary fig. 100. Lanius collurio



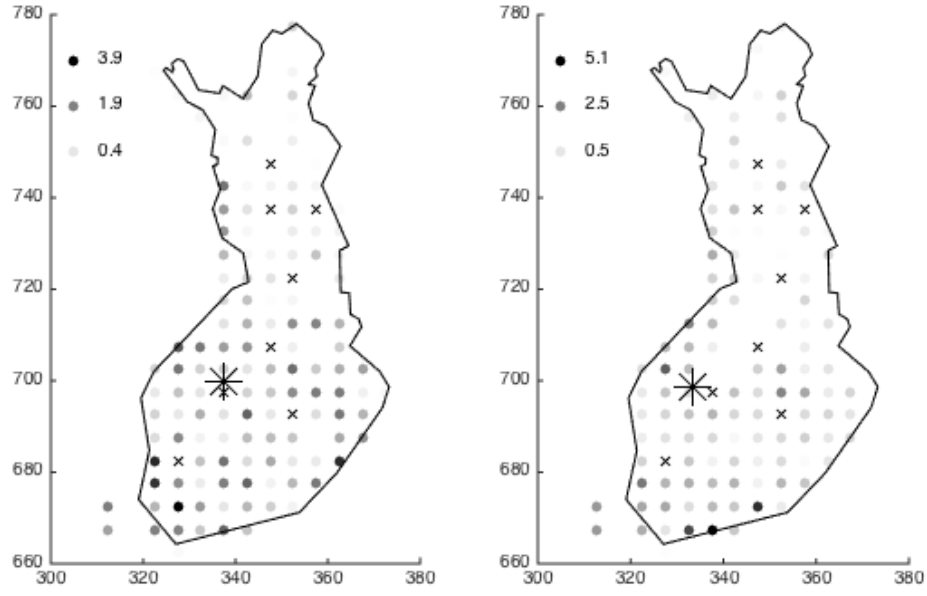
Supplementary fig. 101. Lanius excubitor



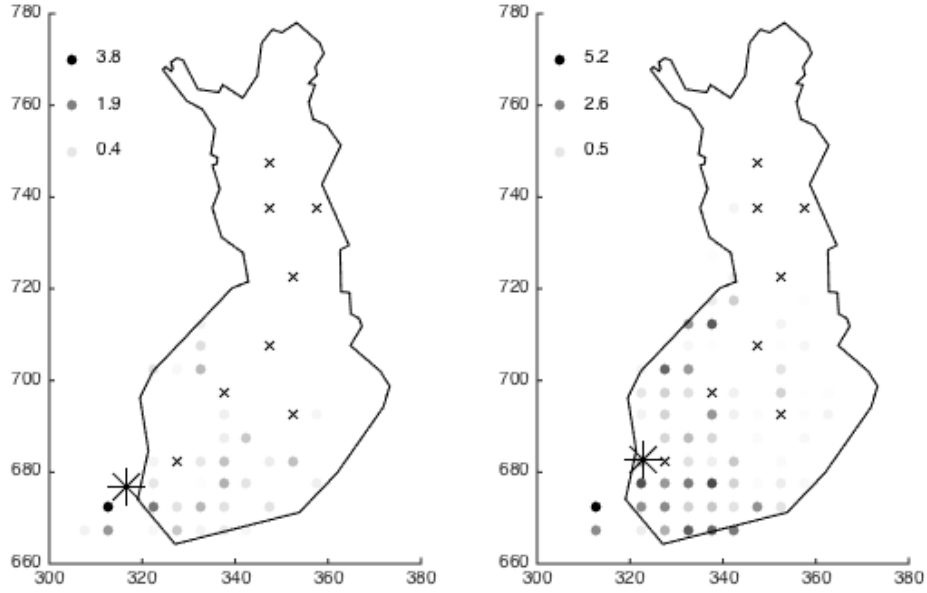
Supplementary fig. 102. Garrulus glandarius



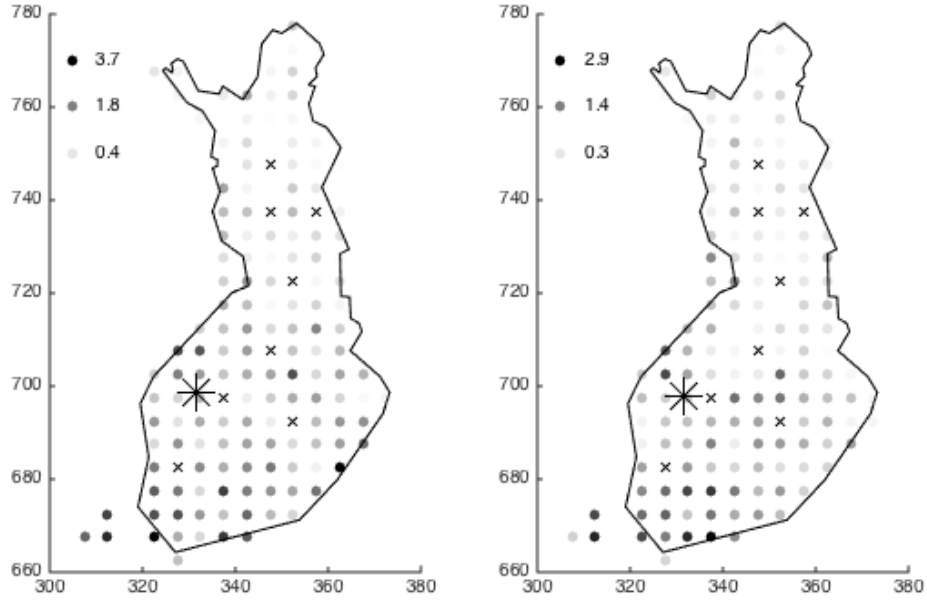
Supplementary fig. 103. Perisoreus infaustus



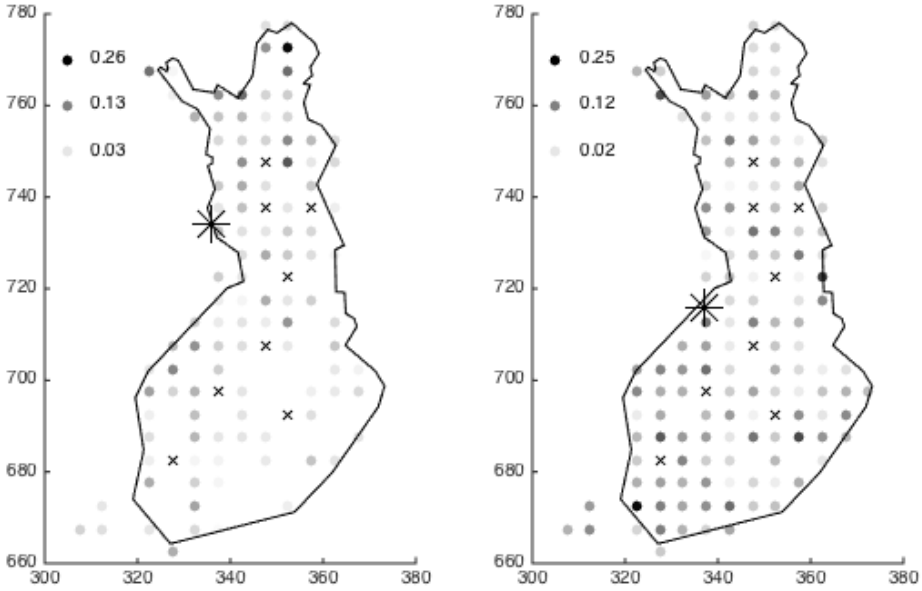
Supplementary fig. 104. Pica pica



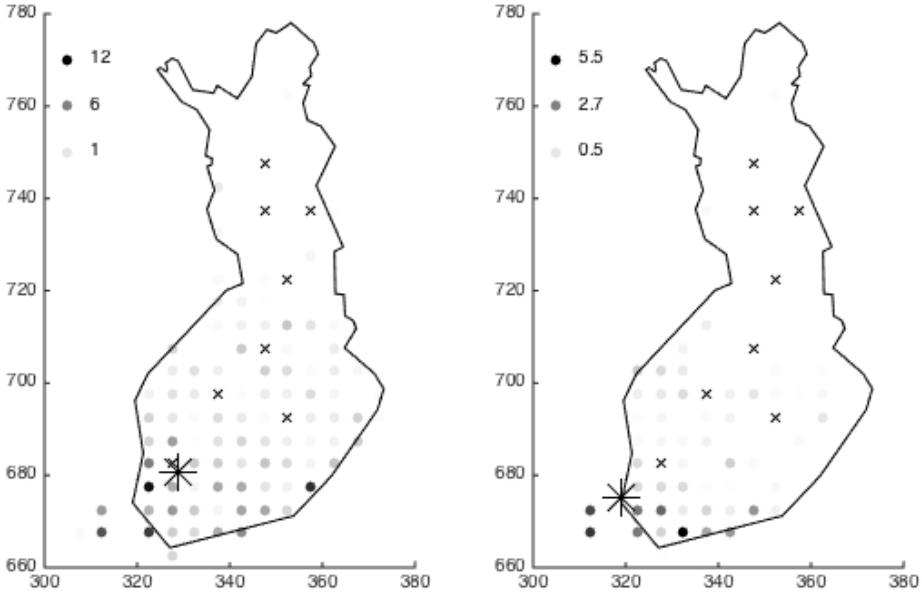
Supplementary fig. 105. Corvus monedula



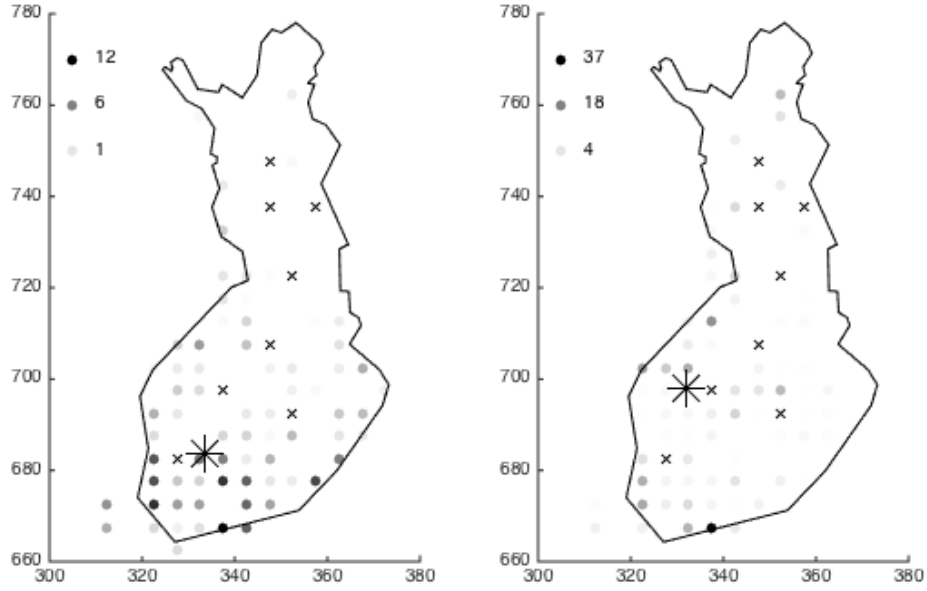
Supplementary fig. 106. Corvus corone



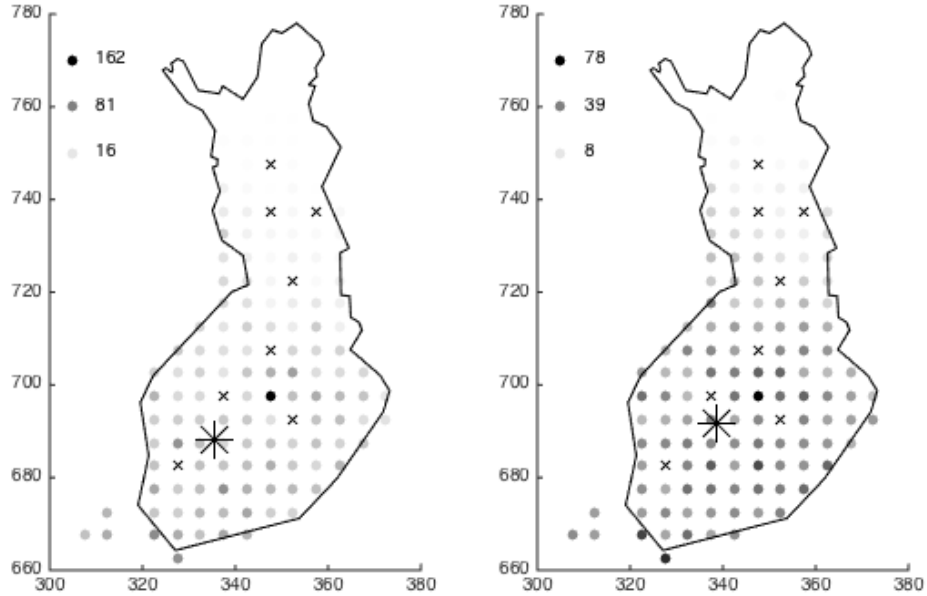
Supplementary fig. 107. Corvus corax



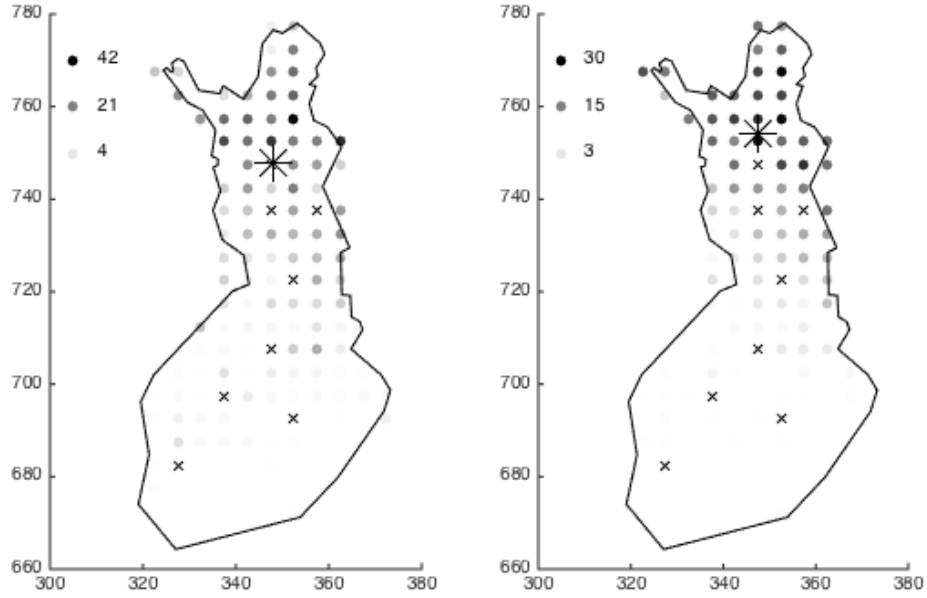
Supplementary fig. 108. Sturnus vulgaris



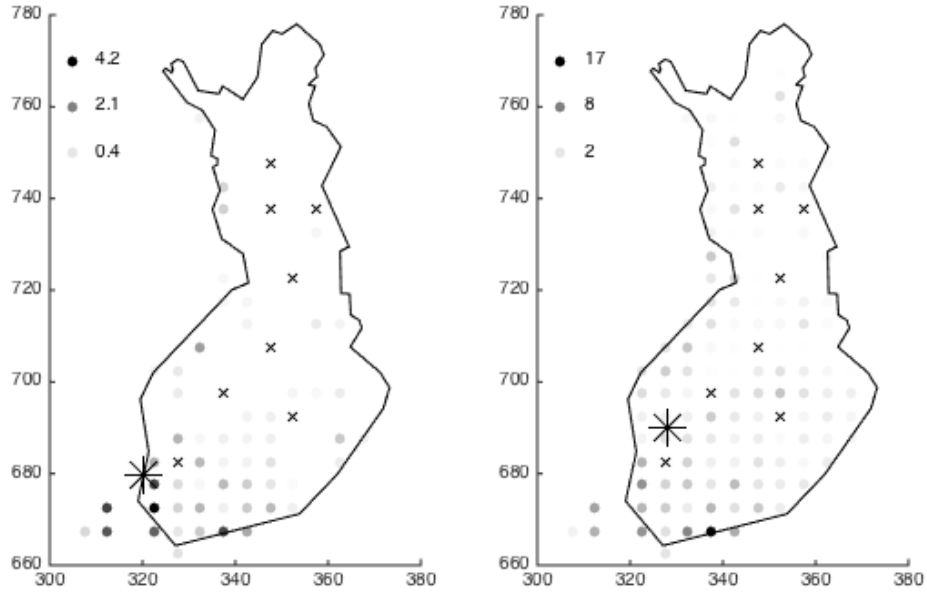
Supplementary fig. 109. Passer domesticus



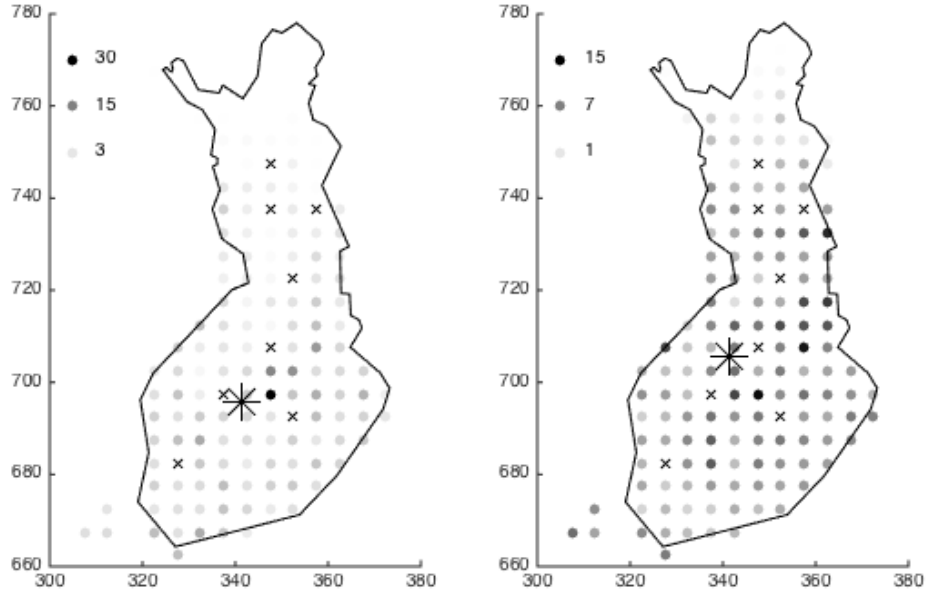
Supplementary fig. 110. Fringilla coelebs



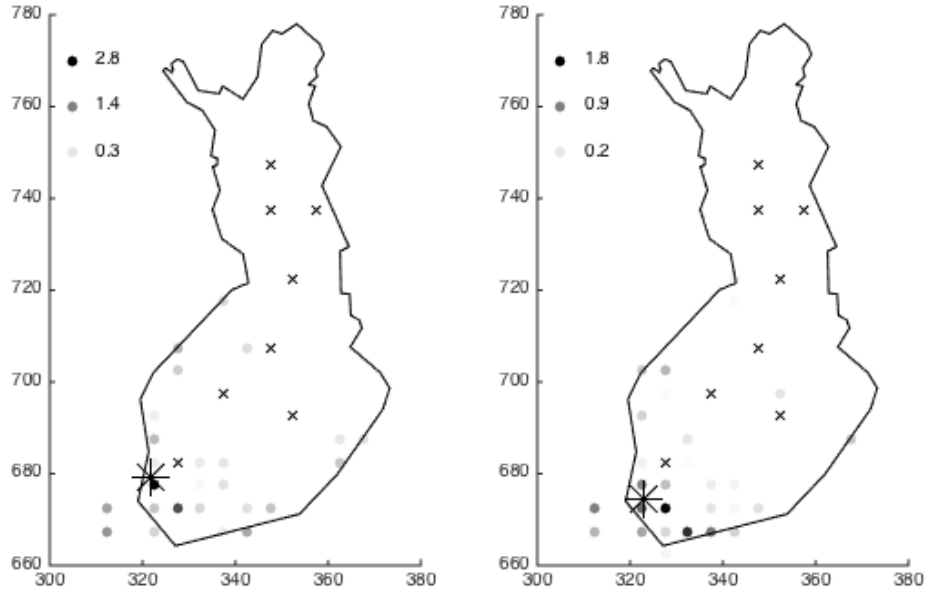
Supplementary fig. 111. Fringilla montifringilla



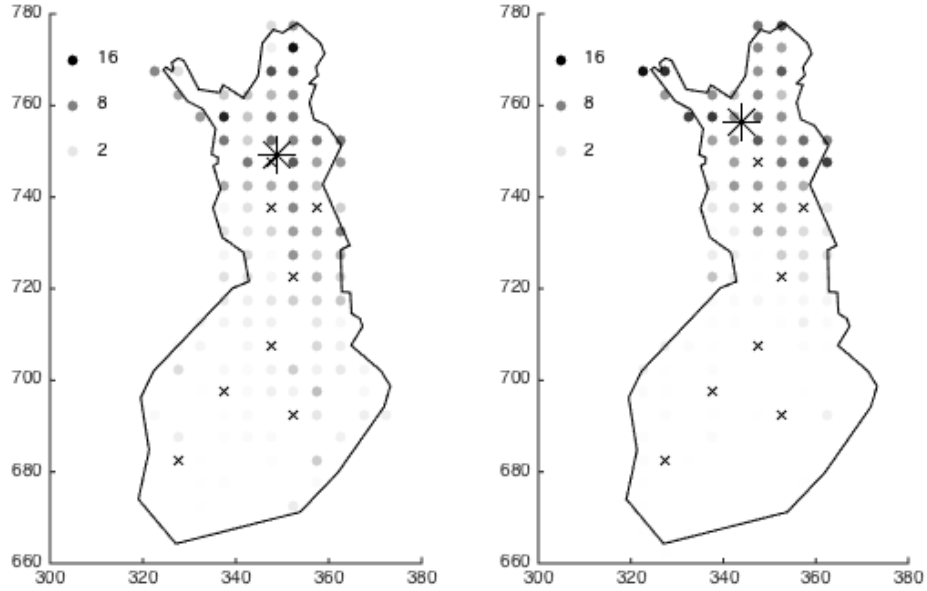
Supplementary fig. 112. Carduelis chloris



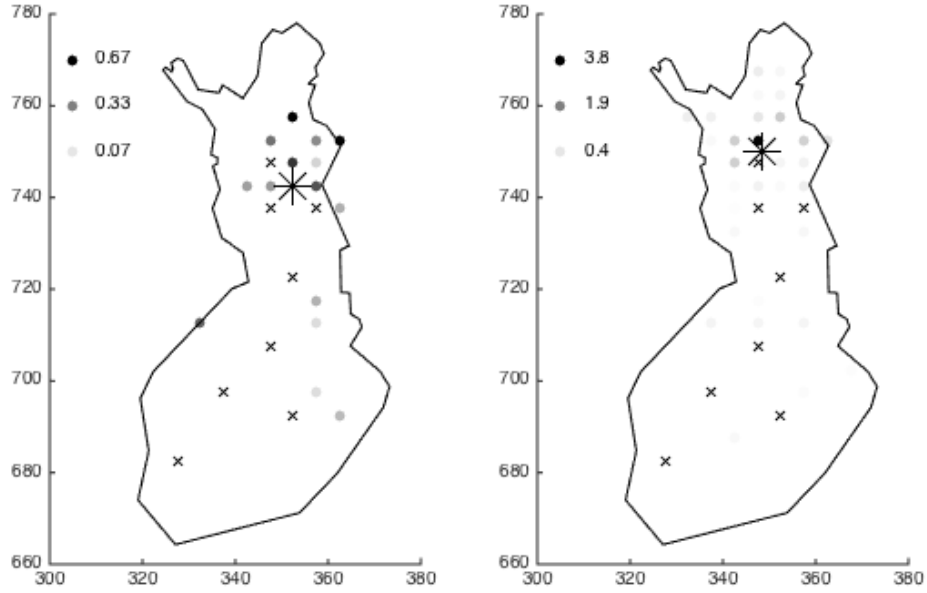
Supplementary fig. 113. Carduelis spinus



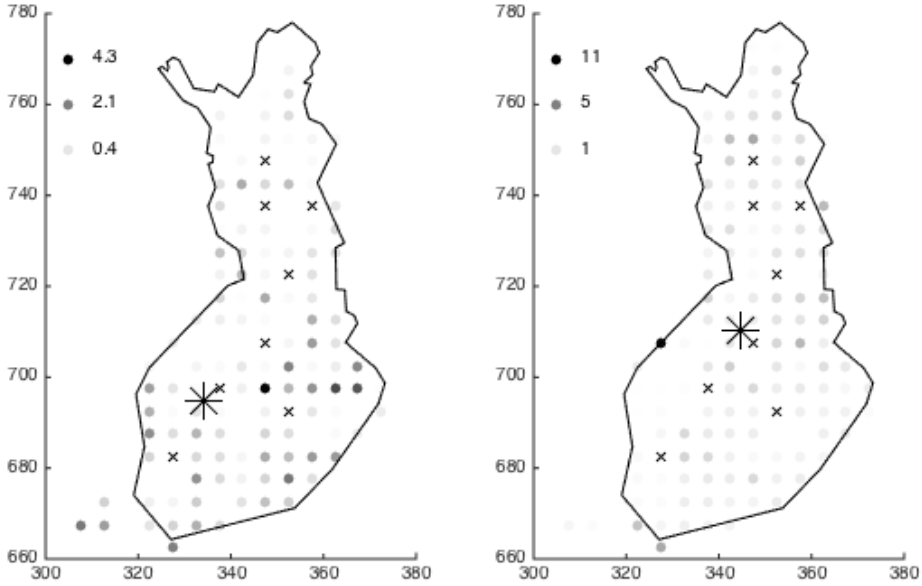
Supplementary fig. 114. Carduelis cannabina



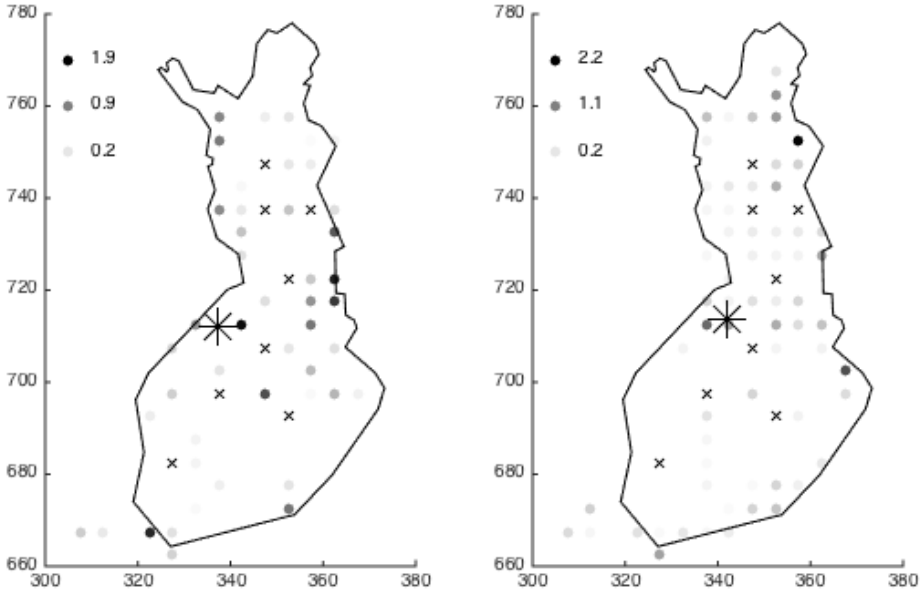
Supplementary fig. 115. Carduelis flammea



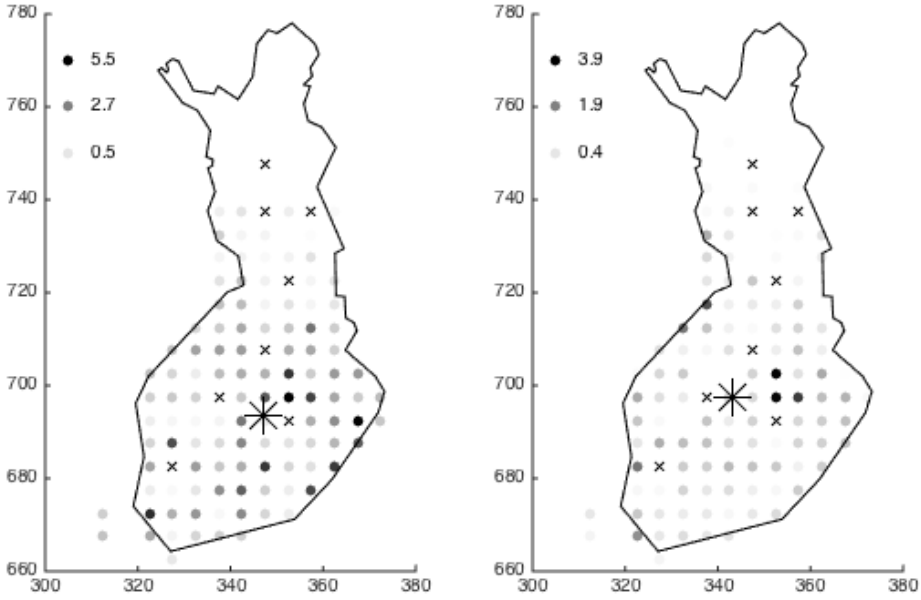
Supplementary fig. 116. Loxia leucoptera



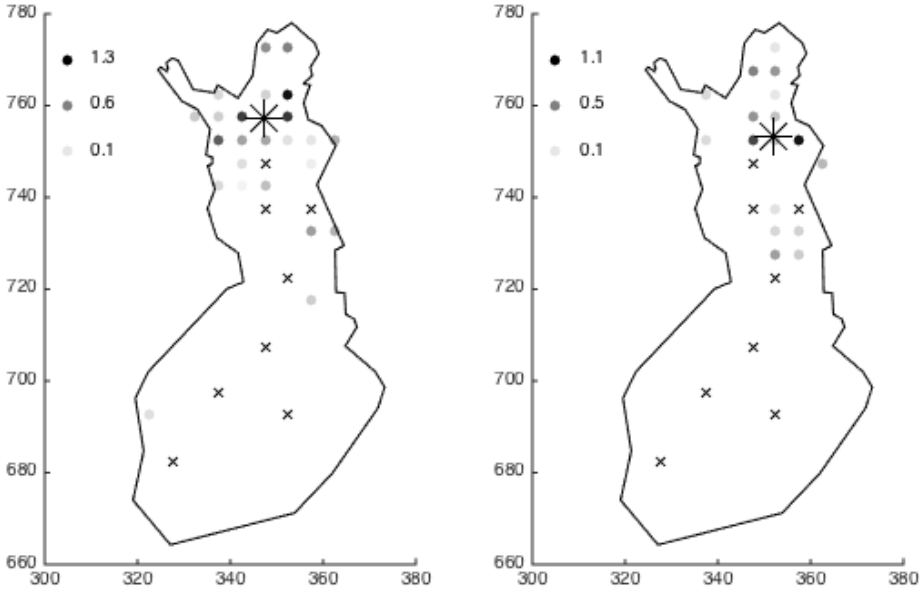
Supplementary fig. 117. Loxia curvirostra



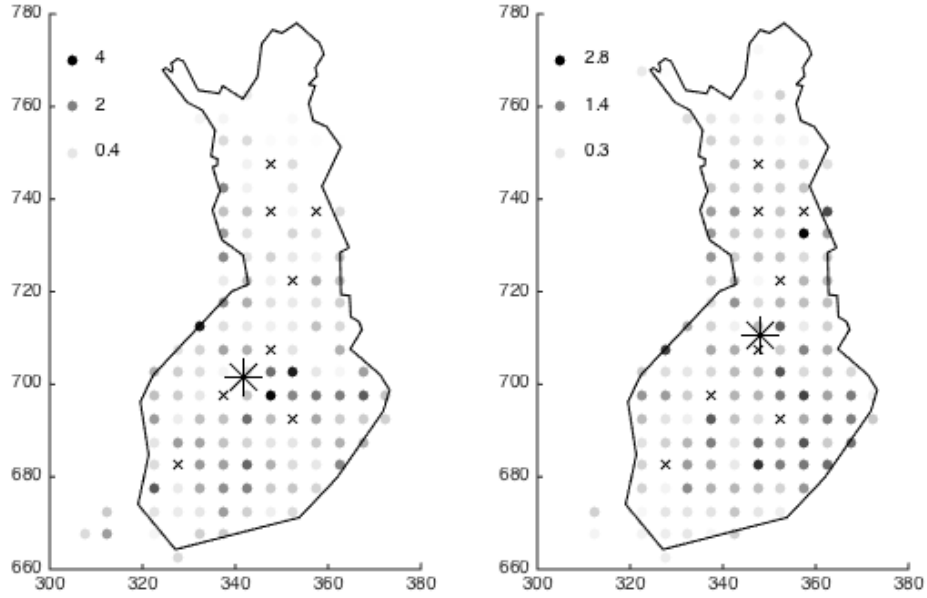
Supplementary fig. 118. Loxia pytyopsittacus



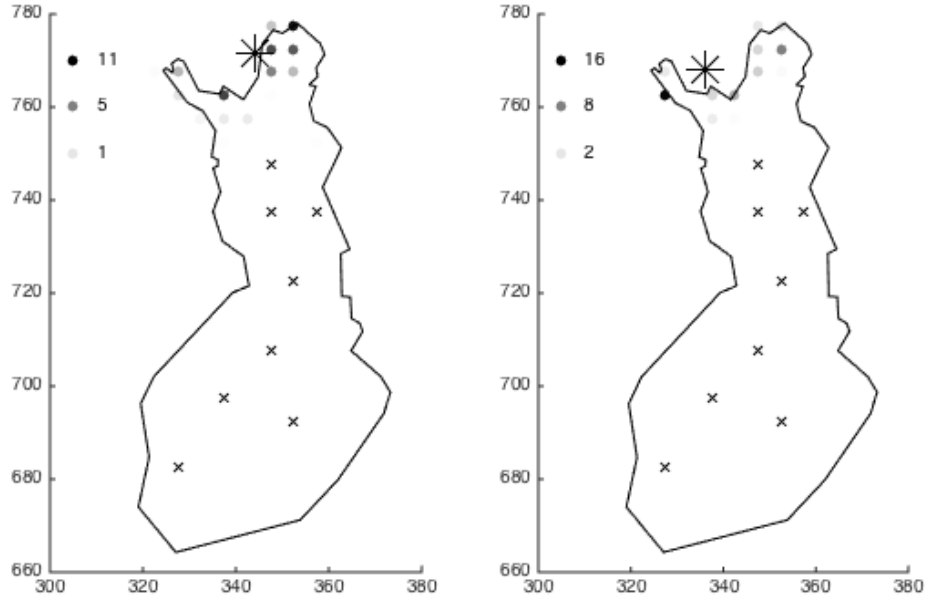
Supplementary fig. 119. Carpodacus erythrinus



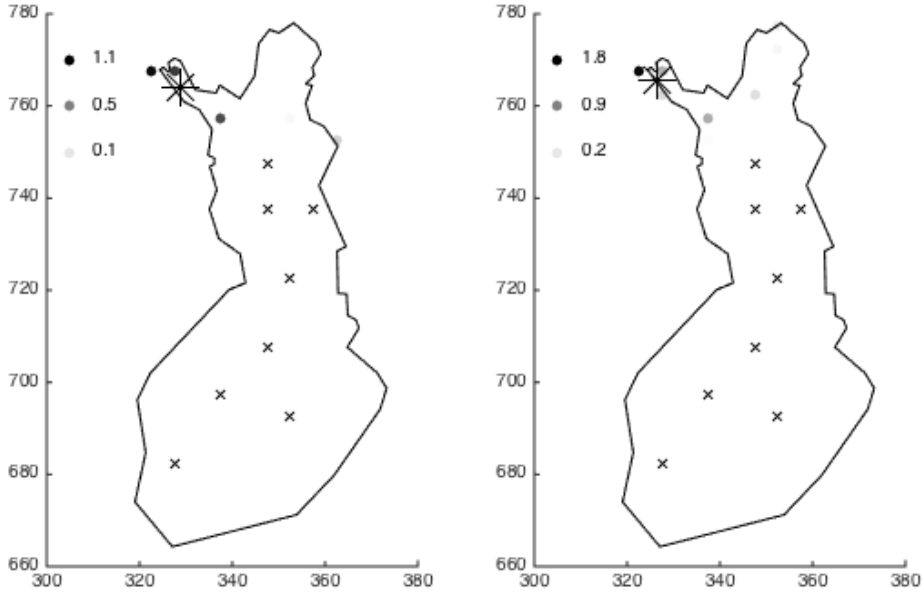
Supplementary fig. 120. Pinicola enucleator



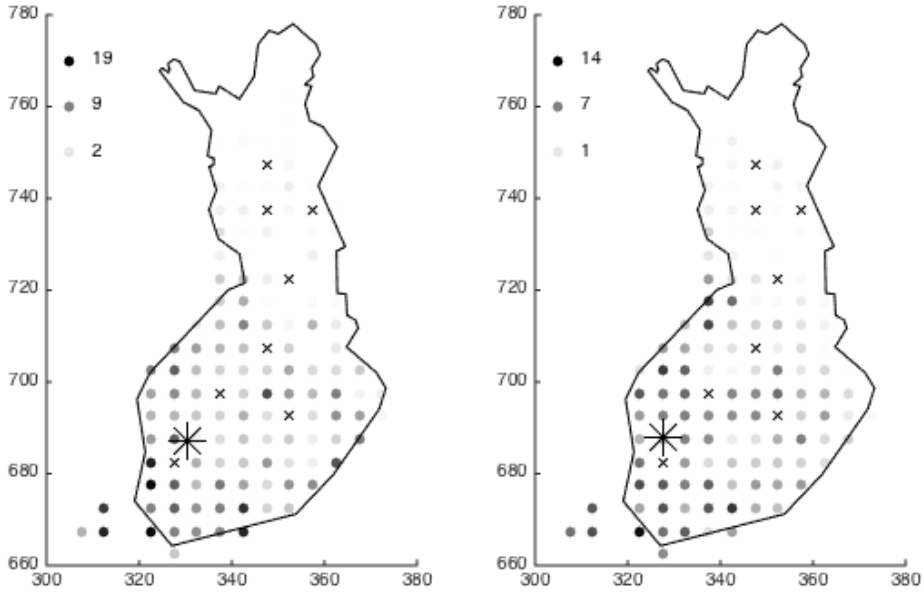
Supplementary fig. 121. Pyrrhula pyrrhula



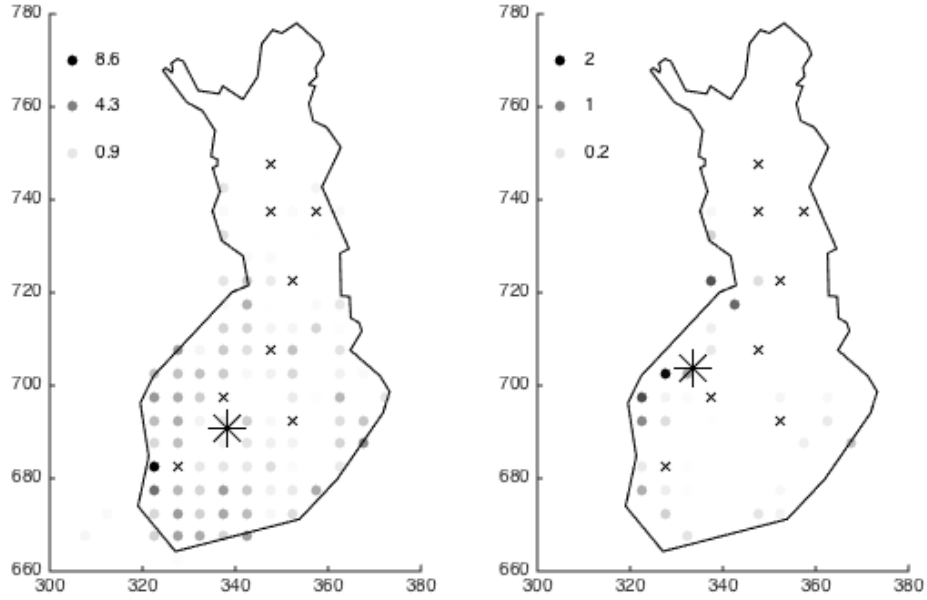
Supplementary fig. 122. Calcarius lapponicus



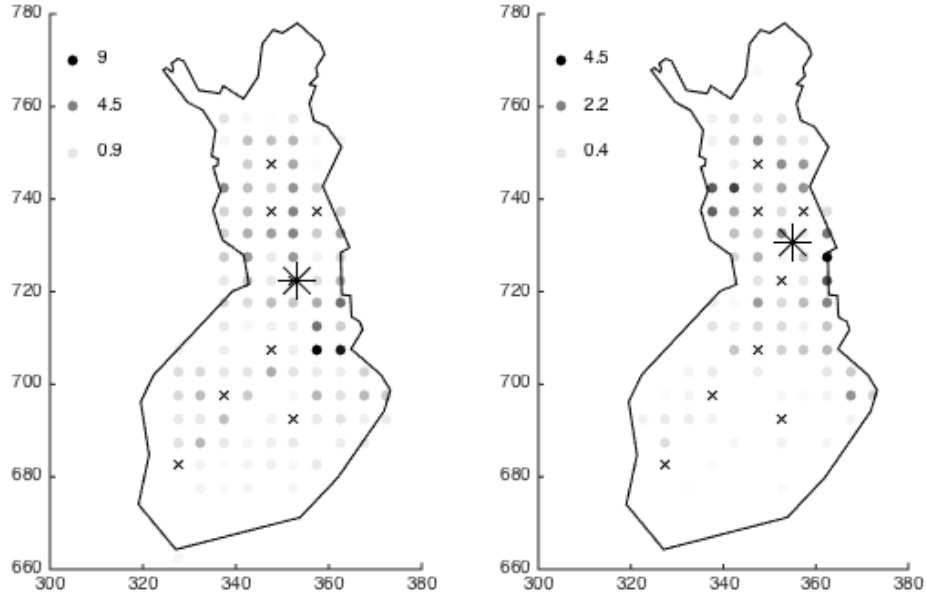
Supplementary fig. 123. Plectrophenax nivalis



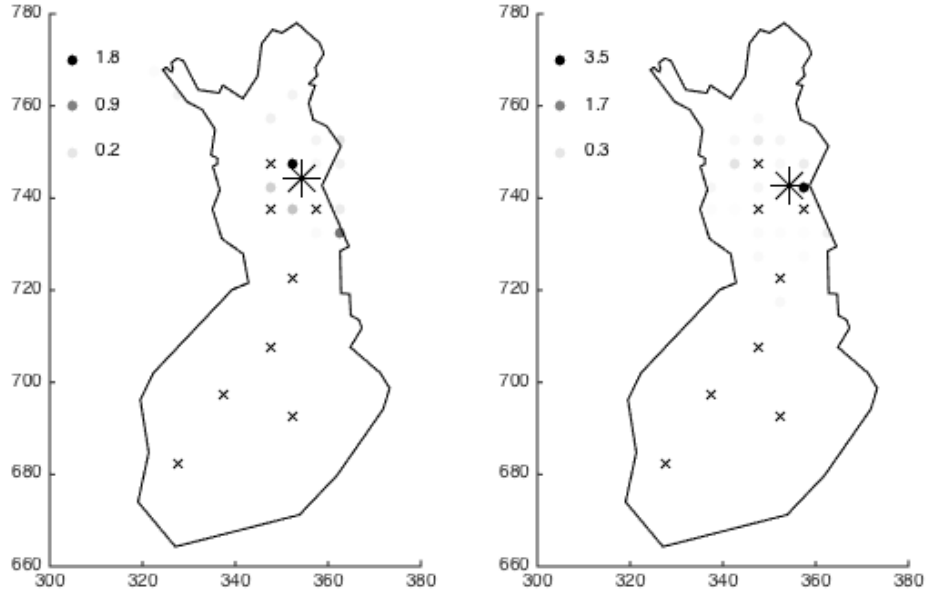
Supplementary fig. 124. Emberiza citrinella



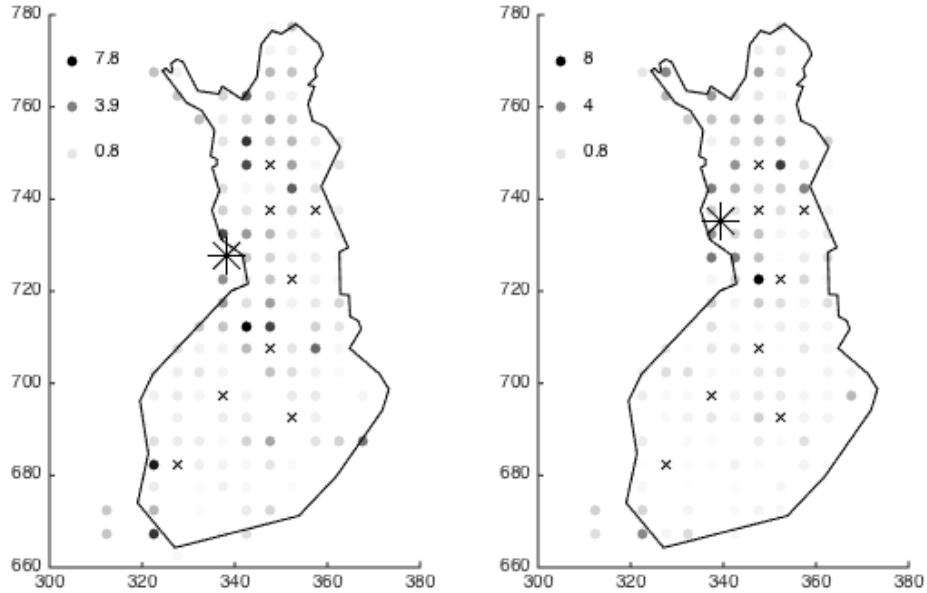
Supplementary fig. 125. Emberiza hortulana



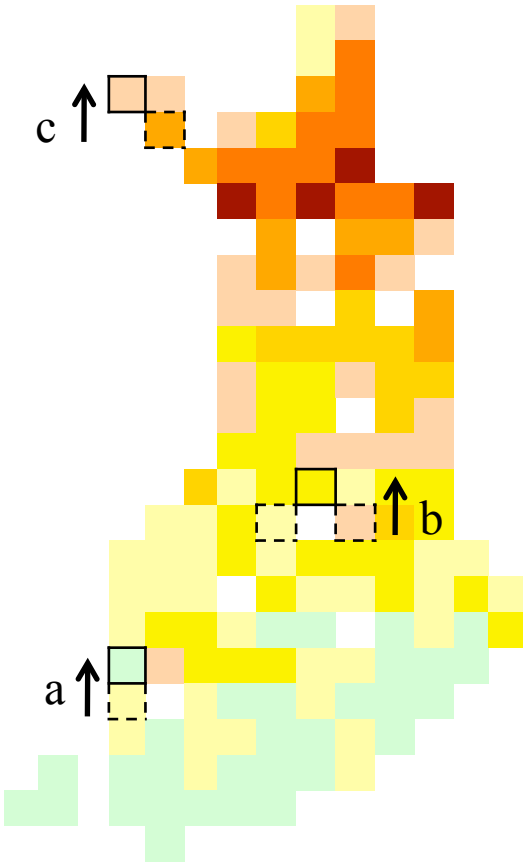
Supplementary fig. 126. Emberiza rustica



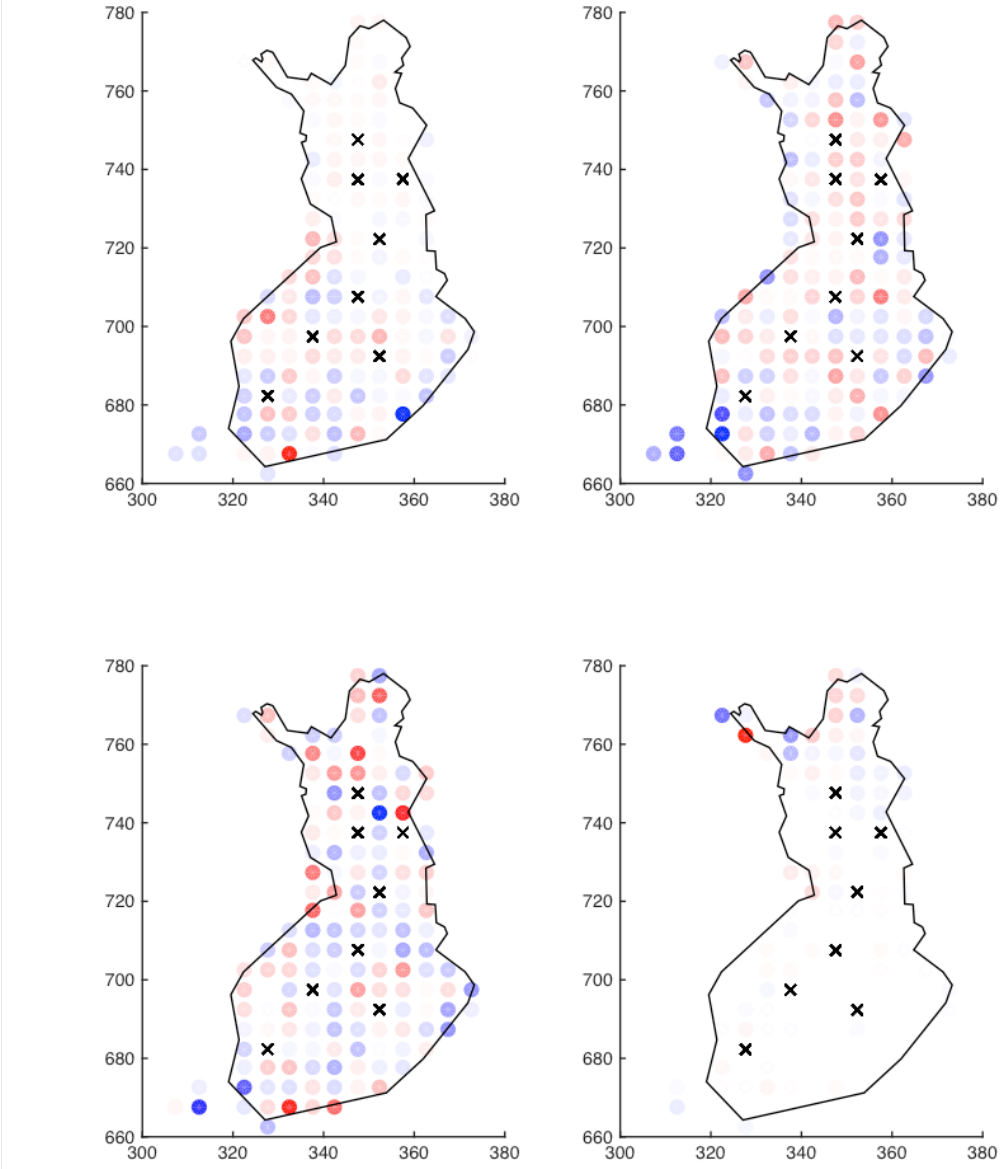
Supplementary fig. 127. Emberiza pusilla



Supplementary fig. 128. Emberiza schoeniclus

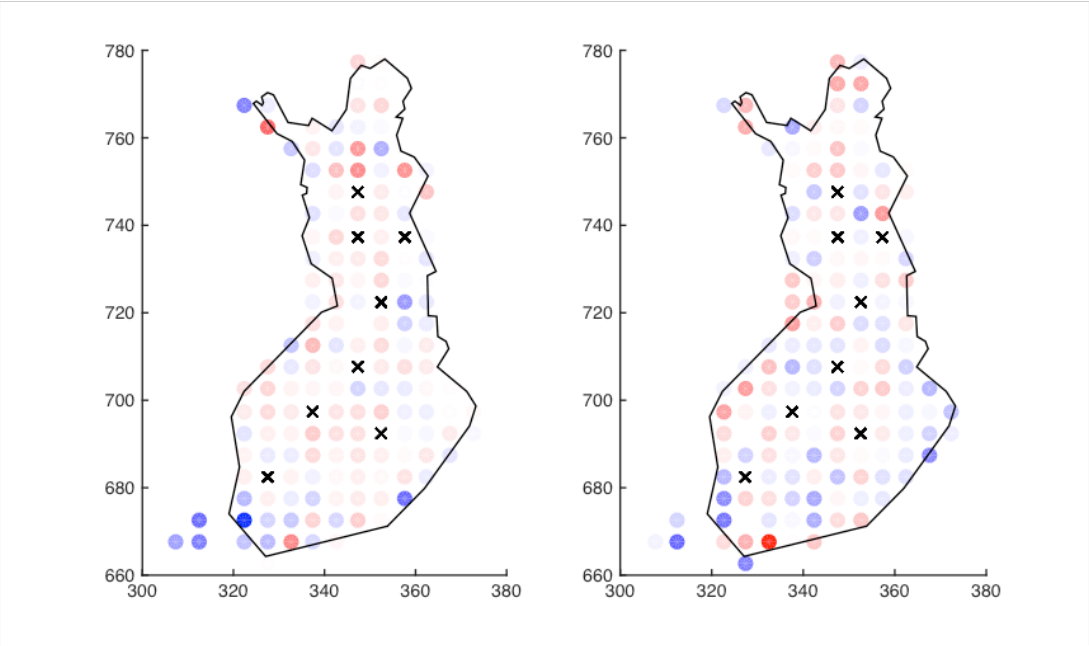


Supplementary Fig. 1. Illustration of how we moved densities of species one grid northwards to estimate the potential effect of shape of the country on the direction of density shifts. In a normal situation (a), the densities were moved one grid northwards. In situations, where the density value was missing from the southern side (b), we used mean of the nearest southwest and southeast grids, or only one of them (c) if both values were not available. The dashed line grids in the figure illustrate the former situation and the solid line grids represents the corresponding grids after the moved densities in Brambling *Fringilla montifringilla* (see also Supplementary Figs 1-129). In case of examples b and c, the densities in the dashed grids were also moved directly northwards like in case a.



Supplementary Fig. 130. Grid specific changes of relative densities of groups of species classified based on their main habitat type: (a) farmland species, (b) forest species, (c) wetland species and (d) montane species. In graphs the species-specific relative densities have been scaled into the same unit in all species so that all species would have equal impact (in contrast to a situation where the most abundant species would dominate the change) corresponding direction analyses (Fig. 1). These grid specific relative densities of species in the first period were subtracted from the corresponding densities

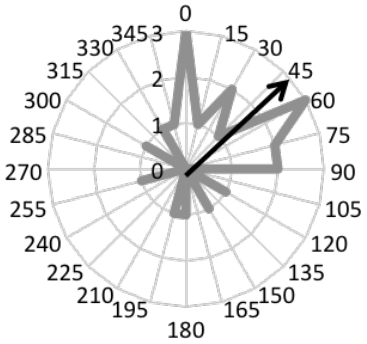
of the latter period. These density changes of the same habitat category were combined grid-specifically and are expressed in colours. Red colour means increasing relative densities and blue declining relative densities. The black crosses show grids without data.



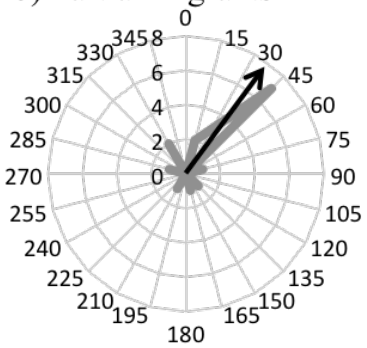
Supplementary Fig. 131. Grid specific changes of relative densities of groups of species classified based on their migration type: (a) residents and partial migrants and (b) short- and long-distance migrants. In graphs the species-specific relative densities have been scaled into the same unit in all species so that all species would have equal impact (in contrast to a situation where the most abundant species would dominate the change) corresponding direction analyses (Fig. 1). These grid-specific relative densities of species in the first period were subtracted from the corresponding densities of the latter period. These density changes of the same migration category were combined grid-specifically

and are expressed in colours. Red colour means increasing relative densities and blue declining relative densities. The black crosses show grids without data.

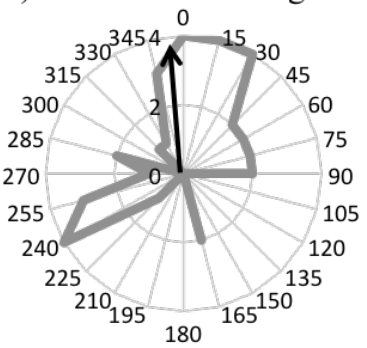
a) Residents



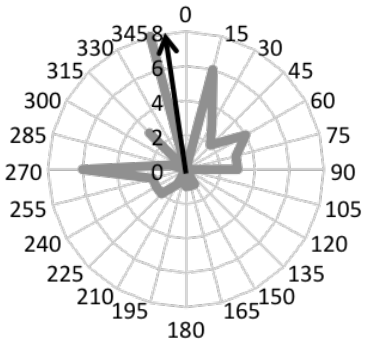
b) Partial migrants



c) Short-distance migrants



d) Long-distance migrants



Supplementary Fig. 132. Distribution of directions of changes in densities based on four migration groups (resident: $\alpha = 43$, partial: $\alpha = 35$, short-distance: $\alpha = 359$, and long-distance migrants: $\alpha = 357$),

Supplementary Table 1. Species-specific sample sizes (N 70-80, N 2000), habitat (Hab), migration (Mig, Mdir) and distribution (Dist) classifications, central gravity of density expressed as latitudes (La70-80, La00) and longitudes (Lo70-80, La00) during both study periods, direction of the density shift (Dir in degrees), total distance of shift (Dist2), density shift along latitude (Ndist) and longitude (Edist) directions (negative values mean shifts towards south and west, respectively) and direction of the species-specific temperature shift. Bolded values in density shifts along latitude and longitude mean that separate Poisson regression analyses of the particular species revealed significant shift in latitude or longitude after Bonferroni correction (note that this is different than changes in the mean central gravity, see more accurately in the text).

Species	N 70-80	N 2000	Hab	Mig	Mdir	Dist	La70-80	La00	Lo70-80	Lo00	Dir (Deg)	Dist2	Ndist	Edist	Tdir (Deg)
Tetrastes bonasia	462	868	2	0	4	2	692.9	701.4	342.9	347.9	30.3	99.1	**85.6**	**50.1**	25.2
Lagopus lagopus	267	293	2	0	4	2	751.0	756.4	343.8	343.2	353.4	54.8	**54.4**	-6.3	350.1
Lagopus muta	43	41	4	0	4	3	766.2	763.5	324.9	326.1	155.6	29.7	-27.0	12.3	325.9
Tetrao tetris	1048	1916	2	0	4	2	699.0	708.9	334.2	344.1	45.3	139.8	98.4	99.4	21.3
Tetrao urogallus	228	418	2	0	4	2	714.6	714.9	347.9	352.1	85.9	42.3	3.0	42.2	14.1
Phasianus colchicus	384	515	1	0	4	2	671.6	683.5	330.3	330.2	359.4	119.5	119.5	-1.3	38.0
Pernis apivorus	22	36	2	1	2	2	689.9	690.8	351.4	340.9	274.6	105.9	8.6	-105.5	19.4
Circus cyaneus	45	44	3	1	1	2	725.5	713.7	350.2	341.2	217.6	148.0	-117.3	-90.3	9.5
Accipiter gentilis	60	59	2	0	4	2	699.1	702.2	334.9	335.6	11.5	31.4	30.8	6.3	30.3
Accipiter nisus	40	70	2	1	1	2	698.7	701.3	323.9	338.8	80.1	151.0	25.9	148.7	24.6
Buteo buteo	98	66	2	1	4	2	698.9	684.1	348.7	334.3	224.1	206.1	-148.1	-143.3	22.2
Buteo lagopus	96	66	2	0	3	3	763.0	767.0	341.4	346.5	51.9	64.8	**40.0**	51.0	309.6
Pandion haliaetus	41	54	2	1	2	2	685.8	704.2	333.3	347.2	37.0	230.3	183.9	138.7	18.3
Falco tinnunculus	39	121	1	1	1	2	701.3	728.1	338.7	343.5	10.0	271.9	267.7	47.4	22.8
Falco columbarius	21	32	2	1	1	2	745.3	763.9	333.1	339.2	18.2	195.5	**185.7**	61.2	333.2
Falco subbuteo	21	52	2	1	2	2	697.8	690.4	352.7	342.1	235.6	129.4	-73.1	-106.7	22.5
Grus grus	330	1696	3	1	2	2	710.2	708.4	344.0	333.7	260.3	105.2	-17.8	**-103.7**	20.8
Haematopus ostralegus	31	102	3	1	1	1	674.1	689.5	312.4	317.3	17.7	161.6	153.9	49.1	33.8
Charadrius hiaticula	34	69	4	1	1	2	754.8	758.8	330.2	337.5	61.1	82.9	**40.0**	72.6	310.7
Pluvialis apricaria	1139	1237	4	1	1	2	760.6	759.5	347.8	342.5	258.8	54.3	**-10.6**	-53.3	355.1
Vanellus vanellus	1308	2201	1	1	1	2	691.8	691.6	338.3	331.9	267.9	64.0	**-2.3**	-64.0	25.6
Calidris pugnax	407	156	3	1	1	3	746.3	750.2	344.5	345.6	15.6	40.2	**38.8**	10.8	351.0
Calidris falcinellus	114	206	3	1	3	3	751.1	752.1	339.4	343.4	76.3	41.4	**9.8**	40.2	328.1
Lymnocryptes minumus	205	172	3	0	1	3	754.1	752.6	346.5	345.7	207.8	17.0	**-15.0**	-7.9	334.4
Gallinago gallinago	1836	2146	3	1	1	2	723.7	729.8	338.2	342.2	33.3	72.5	**60.6**	39.7	12.6
Scolopax rusticola	158	440	2	1	1	2	690.7	691.5	327.3	334.1	83.4	67.6	**7.8**	67.2	28.9
Numenius phaeopus	1130	755	3	1	1	2	744.7	755.3	353.9	350.1	340.2	112.5	**105.9**	-38.2	352.0
Numenius arquata	1734	2744	1	1	1	2	703.5	705.6	341.4	341.5	4.1	21.1	21.0	1.5	26.5
Tringa erythropus	222	135	3	1	2	3	758.8	756.6	345.7	347.1	148.2	26.0	**-22.1**	13.7	332.2
Tringa totanus	313	342	3	1	1	2	701.5	712.6	316.0	320.9	23.5	121.3	111.3	48.4	35.6
Tringa nebularia	737	1284	3	1	2	2	733.1	730.1	355.1	352.8	217.3	38.8	-30.8	-23.5	4.0

Tringa ochropus	683	2394	2	1	1	2	689.6	697.4	345.6	338.5	317.9	105.6	**78.3**	-70.8	23.2
Tringa glareola	2970	3803	3	1	2	2	740.9	747.5	347.8	346.2	346.4	67.2	**65.3**	-15.8	7.0
Actitis hypoleucos	303	356	3	1	2	2	707.6	722.5	336.1	339.1	11.2	151.5	148.6	29.5	16.5
Phalaropus lobatus	85	34	3	1	3	3	758.9	762.1	341.0	338.1	317.1	43.3	**31.7**	-29.5	326.1
Stercorarius longicaudus	33	49	4	1	1	3	767.2	773.4	338.6	346.9	53.2	104.0	**62.3**	83.3	326.4
Columba livia	102	561	1	0	4	1	674.9	687.5	347.3	329.6	305.4	216.9	125.7	-176.8	20.9
Columba oenas	382	302	1	1	1	1	670.1	670.3	314.2	319.1	88.0	48.4	1.7	48.4	41.9
Columba palumbus	3682	8195	1	1	1	2	686.7	686.4	330.9	330.2	240.2	7.7	**-3.8**	**-6.7**	28.2
Cuculus canorus	4650	7760	2	1	2	2	710.5	711.0	339.5	345.2	85.5	57.5	**4.5**	**57.4**	14.0
Surnia ulula	27	25	2	0	4	3	740.5	744.3	345.9	349.9	46.8	55.6	38.1	40.5	327.5
Asio flammeus	66	69	3	1	1	2	740.4	753.8	343.5	340.6	347.5	137.2	**134.0**	-29.7	357.5
Apus apus	1231	2086	1	1	2	2	684.3	688.8	331.7	335.7	41.6	60.0	**44.9**	39.8	26.9
Jynx torquilla	376	206	2	1	1	2	696.7	707.1	337.7	334.1	340.9	110.2	104.1	-36.1	17.2
Picus canus	29	36	2	0	4	2	669.1	673.7	317.6	327.6	64.9	109.5	46.5	99.1	38.2
Dryocopus martius	270	1043	2	0	4	2	688.6	694.0	330.5	334.1	33.7	64.8	**53.9**	35.9	18.1
Dendrocopos major	1326	3648	2	0	4	2	694.8	702.4	341.8	338.3	335.3	83.5	**75.8**	-34.9	26.1
Dendrocopos minor	30	37	2	0	4	2	688.9	680.8	321.4	334.3	122.0	152.1	-80.5	129.0	27.8
Picoides tridactylus	74	148	2	0	4	2	735.7	730.6	351.5	349.9	197.2	53.4	-51.0	-15.8	337.5
Lullula arborea	31	101	2	1	1	1	668.1	666.3	325.4	316.1	259.2	95.2	-17.8	**-93.5**	34.6
Alauda arvensis	3912	3581	1	1	1	2	684.8	685.5	327.9	323.2	278.2	46.7	**6.7**	**-46.2**	25.7
Riparia riparia	341	532	3	1	2	2	714.5	713.3	353.7	348.5	256.9	52.5	-11.9	-51.2	16.2
Hirundo rustica	1552	1761	1	1	2	2	693.3	693.3	339.7	334.9	270.9	47.5	**0.7**	-47.5	26.9
Delichon urbicum	1031	758	1	1	2	2	687.2	697.1	338.1	336.0	347.8	101.6	99.4	-21.4	26.0
Anthus trivialis	15580	18958	2	1	2	2	700.5	701.3	340.2	342.6	71.0	25.9	**8.4**	24.4	16.4
Anthus prantensis	5147	4754	3	1	1	2	750.6	755.3	343.4	340.6	329.7	55.2	**47.7**	**-27.8**	8.7
Motacilla flava	4301	2805	3	1	1	2	735.2	748.7	349.0	345.5	345.6	139.4	**135.0**	-34.7	12.0
Motacilla alba	2283	3315	3	1	2	2	696.7	695.2	335.2	332.6	241.2	30.6	**-14.7**	**-26.8**	16.9
Bombycilla garrulus	73	611	2	0	4	2	737.8	741.9	353.6	355.0	18.8	43.3	**41.0**	14.0	326.3
Troglodytes troglodytes	289	1371	2	1	1	2	678.4	684.0	347.0	330.3	288.4	176.9	**55.9**	-167.8	22.5
Prunella modularis	2260	4949	2	1	1	2	686.7	693.0	340.3	343.3	25.5	69.8	**63.0**	**30.1**	23.2
Erithacus rubecula	5127	16046	2	1	1	2	688.4	695.8	338.7	336.7	344.9	77.2	**74.5**	-20.1	23.1
Luscinia luscinia	288	574	3	1	2	2	673.3	672.3	325.5	334.0	96.3	86.2	**-9.5**	85.7	31.5
Luscinia svecica	862	930	4	1	3	3	764.7	768.4	335.2	336.6	20.8	39.5	**36.9**	14.0	312.3
Phoenicurus phoenicurus	4109	7841	2	1	1	2	730.3	735.8	346.2	350.2	35.6	68.1	**55.4**	39.6	14.1
Saxicola rubetra	1687	1601	1	1	1	2	703.4	711.2	342.2	341.0	351.2	78.6	77.7	-12.1	16.8
Oenanthe oenanthe	1467	594	3	1	1	2	738.1	747.3	336.7	338.7	12.5	94.1	**91.9**	20.4	12.0
Turdus torquatus	25	35	4	1	1	3	769.9	768.5	326.1	326.4	169.0	14.0	-13.8	2.7	331.0

Turdus merula	2108	6764	2	0	1	2	672.8	677.8	319.0	324.9	49.4	77.5	**50.5**	**58.8**	32.2
Turdus pilaris	5173	13779	1	1	1	2	694.5	697.9	339.4	338.9	351.6	33.5	**33.1**	-4.9	16.1
Turdus philomelos	6892	13336	2	1	1	2	695.8	701.4	335.4	339.8	38.1	70.3	**55.3**	**43.3**	17.3
Turdus iliacus	12476	14609	2	1	1	2	713.8	724.3	341.4	342.7	7.1	106.2	105.4	13.2	13.7
Turdus viscivorus	448	1675	2	1	2	2	705.4	706.7	333.2	336.4	68.6	34.5	12.6	32.1	16.2
Locustella naevia	20	39	3	1	1	2	681.0	685.3	337.2	337.8	8.0	43.4	43.0	6.0	22.4
Acrocephalus schoenobaenus	1234	1691	3	1	2	2	701.6	701.9	339.9	332.8	273.0	71.1	3.8	-71.0	18.5
Acrocephalus dumetorum	51	176	3	1	3	2	686.6	682.4	363.6	352.0	249.8	124.2	**-42.9**	-116.6	17.1
Acrocephalus palustris	39	86	3	1	2	2	672.5	671.3	331.0	316.7	265.3	144.0	**-11.8**	-143.5	19.8
Acrocephalus scirpaceus	349	265	3	1	1	1	668.7	668.6	315.5	316.9	97.0	14.0	-1.7	13.9	33.7
Hippolais icterina	164	182	2	1	2	2	667.2	670.2	321.2	324.9	50.8	47.7	**30.1**	36.9	25.9
Sylvia curruca	1467	2885	2	1	2	2	689.0	689.9	338.7	334.7	283.3	41.7	**9.6**	-40.6	27.4
Sylvia communis	1939	3147	1	1	2	2	677.9	678.0	329.0	328.3	273.3	7.5	**0.4**	-7.5	30.1
Sylvia borin	6484	9260	2	1	2	2	685.9	687.4	337.2	340.5	66.6	35.5	**14.1**	32.6	26.9
Sylvia atricapilla	628	1334	2	1	2	2	672.3	671.9	317.4	316.8	229.1	7.3	**-4.8**	**-5.5**	31.6
Phylloscopus trochiloides	88	216	2	1	3	2	681.8	679.1	348.1	341.9	246.9	67.8	-26.6	-62.3	22.4
Phylloscopus sibilatrix	2475	1966	2	1	1	2	680.1	682.8	342.1	343.9	33.0	32.1	**26.9**	17.4	26.7
Phylloscopus collybita	2430	3336	2	1	2	2	685.7	687.8	330.9	332.3	34.2	25.4	**21.0**	14.3	29.3
Phylloscopus trochilus	58187	76890	2	1	2	2	711.8	716.5	343.2	342.3	349.0	47.9	47.0	-9.1	13.7
Regulus regulus	3122	5344	2	0	1	2	684.5	689.5	330.2	331.0	9.0	50.7	**50.1**	8.0	26.0
Muscicapa striata	4340	6815	2	1	2	2	700.1	701.5	337.3	340.4	65.8	33.6	**13.8**	30.6	16.9
Ficedula parva	43	125	2	1	3	2	669.0	680.5	330.2	353.8	64.0	262.6	**115.2**	235.9	31.4
Ficedula hypoleuca	3157	6607	2	1	1	2	702.9	698.2	337.1	338.2	166.7	48.6	**-47.3**	11.2	16.7
Poecile montanus	2744	3700	2	0	4	2	697.4	706.2	333.4	346.2	55.7	155.0	**87.4**	128.0	18.7
Poecile cinctus	223	152	2	0	4	3	757.1	758.6	345.6	348.1	59.4	28.7	**14.6**	24.7	316.0
Lophophanes cristatus	1071	2169	2	0	4	2	681.8	683.4	329.8	342.0	82.8	122.6	**15.3**	121.6	28.8
Periparus ater	398	690	2	0	1	2	670.9	673.8	312.6	327.7	79.1	154.1	**29.0**	151.3	34.5
Cyanistes caeruleus	442	4257	2	0	1	2	671.0	681.3	319.1	327.7	39.7	134.6	**103.6**	85.9	25.6
Parus major	3815	13145	2	0	1	2	685.4	690.5	329.0	332.6	34.5	62.2	**51.2**	35.2	21.1
Certhia familiaris	523	1245	2	0	1	2	676.0	684.5	323.7	330.5	39.0	109.2	**84.8**	68.8	25.9
Oriolus oriolus	98	37	2	1	2	1	680.1	680.3	352.3	350.1	274.2	22.1	1.6	-22.0	25.3
Lanius collurio	352	335	1	1	2	2	676.0	677.8	329.9	336.3	74.6	67.0	**17.8**	**64.6**	27.9
Lanius excubitor	38	51	2	1	1	2	729.9	731.1	346.8	348.9	60.4	23.7	11.7	20.6	359.3
Garrulus glandarius	534	936	2	0	4	2	686.1	687.1	334.6	338.1	74.0	36.5	**10.1**	35.1	31.3
Perisoreus infaustus	264	339	2	0	4	2	743.7	752.0	351.8	348.8	340.0	88.3	**83.0**	-30.1	334.6
Pica pica	1397	2978	1	0	4	2	700.0	698.6	337.4	333.2	252.1	43.6	**-13.4**	-41.5	19.6
Corvus monedula	452	2663	1	0	1	2	676.9	682.9	316.8	322.7	44.8	84.8	**60.2**	**59.7**	36.6

Corvus corone	4179	5956	1	0	1	2	698.8	697.8	331.4	331.6	166.5	10.0	**-9.7**	**2.3**	15.6
Corvus corax	448	1129	2	0	4	2	734.2	715.8	336.1	336.9	177.3	184.5	-184.3	8.8	11.4
Sturnus vulgaris	2120	1165	1	1	1	2	680.7	675.2	328.9	319.2	240.3	111.2	**-55.0**	**-96.6**	29.2
Passer domesticus	1291	3970	1	0	4	2	683.6	697.8	333.4	331.8	353.7	142.4	141.5	-15.7	25.2
Fringilla coelebs	40860	72779	2	1	1	2	688.0	691.5	335.4	338.5	42.1	46.6	**34.5**	31.2	20.3
Fringilla montifringilla	17398	13105	2	1	1	2	747.8	754.1	348.1	347.4	353.7	64.0	**63.6**	-7.0	8.2
Carduelis chloris	575	5110	1	0	1	2	679.7	689.9	320.2	328.2	37.8	129.8	**102.5**	**79.6**	27.5
Carduelis spinus	7562	20079	2	1	1	2	695.7	705.7	341.2	341.2	359.9	100.4	**100.4**	**-0.2**	19.7
Carduelis cannabina	101	180	1	1	1	1	679.0	674.5	321.9	323.0	166.7	47.1	-45.8	**10.8**	33.6
Carduelis flammea	6215	5976	2	0	3	2	749.3	756.5	348.8	343.9	325.5	87.0	**71.7**	-49.2	4.4
Loxia leucoptera	123	113	2	0	4	3	742.5	749.8	352.5	348.5	331.8	82.8	73.0	-39.2	338.5
Loxia curvirostra	1868	4196	2	0	4	2	694.9	710.3	334.2	344.8	34.3	186.7	154.2	105.2	17.8
Loxia pytyopsittacus	213	295	2	0	4	2	712.2	713.6	337.4	342.0	72.7	47.9	14.2	45.7	13.2
Carpodacus erythrinus	2177	1952	3	1	3	2	693.6	697.4	347.0	343.0	313.5	54.8	**14.2**	45.7	28.9
Pinicola enucleator	107	62	2	0	4	3	757.1	753.1	347.3	351.8	131.5	60.8	**37.7**	-39.7	319.5
Pyrrhula pyrrhula	1169	2121	2	0	4	2	701.7	710.7	341.9	348.1	34.8	109.4	**-40.3**	45.5	21.0
Calcarius lapponicus	337	497	4	1	3	3	771.5	768.2	343.9	336.0	247.0	86.4	**89.8**	**62.4**	307.2
Plectrophenax nivalis	92	97	4	1	3	3	763.8	765.6	328.8	326.6	308.9	28.5	**-33.8**	-79.5	325.9
Emberiza citrinella	6044	9415	1	0	1	2	687.0	687.9	330.4	327.6	286.8	30.2	**17.9**	**-22.2**	21.9
Emberiza hortulana	1119	182	1	1	1	2	690.8	703.6	338.3	333.7	340.1	135.6	8.7	-28.9	29.2
Emberiza rustica	916	554	3	1	3	2	722.3	730.5	353.1	354.9	12.2	84.3	127.5	-46.2	12.2
Emberiza pusilla	77	106	3	1	3	3	744.2	742.6	354.4	354.4	180.5	16.5	82.4	17.8	319.6
Emberiza schoeniclus	1907	2490	3	1	1	2	727.8	735.2	338.2	339.5	9.6	74.8	**-16.5**	-0.1	10.3